COMPETITION AND SELECTIVITY IN THE VISUAL SYSTEM:

EVIDENCE FROM EVENT-RELATED BRAIN POTENTIALS

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COMPETITION AND SELECTIVITY IN THE VISUAL SYSTEM:

EVIDENCE FROM EVENT-RELATED BRAIN POTENTIALS

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LIST OF SYMBOLS AND ABBREVIATIONS

°	Degree of visual angle
BOLD	Blood-oxygen level dependent
EEG	Electroencephalogram
IT	Inferotemporal cortex
MEG	Magnetoencephalogram
MT	Medial temporal cortex
TEO	Visual area in inferotemporal cortex
TE	Visual area in inferotemporal cortex
V1	Primary visual cortex/striate cortex
V2	Visual area in extrastriate cortex
V4	Visual area in extrastriate cortex

SUMMARY

When multiple objects are present in a visual scene, salient and behaviorally relevant objects are selectively processed at the expense of less salient or irrelevant objects. Here I used three lateralized components of the event-related potential – the N2pc, Ptc, and SPCN – to examine how objects compete for representation in our limited capacity visual system, and how task-relevant objects are selectively processed. Participants responded to the orientation of a color singleton target while ignoring a color singleton distractor. Competition between the objects was manipulated by presenting visual search arrays that contained only a target, only a distractor, or both objects together. In Experiment 1, observers did not know the color of the target in advance, whereas in Experiment 2 this information was provided. Experiment 3 was a control experiment to rule out low-level sensory explanations of the effects. The results suggest that the N2pc component indexes capture of attention by salient objects which is modulated both by competition between the objects and top-down knowledge. The Ptc component may index inhibition of return so that once an object is processed it is not selected again. The SPCN component may index enhancement of goal-relevant objects once task-irrelevant objects have been suppressed. Together these lateralized event-related potentials reveal the temporal dynamics of competition and selectivity in the human visual system.

CHAPTER 1

INTRODUCTION

A typical visual scene includes many objects, yet we are only subjectively aware of a small subset of those objects at any given time. Even though the optical information about the scene impinges on our retina and is transduced by the photoreceptors, only a small amount of the available information is processed to the level of consciousness. There is a great deal of evidence that the selection of visual information for higher visual processing is not random; objects that are salient or relevant to current goals are more likely to be represented than less salient, irrelevant, or distracting information. Our ability to selectively process some objects at the expense of others is known as visual selective attention. It is a major goal of researchers studying visual attention to understand why the visual system is limited in capacity and cannot represent every object in the visual scene simultaneously. It is likewise important to understand how salient or goal-relevant information is selected – and how less salient, irrelevant, or distracting information is suppressed – when many objects are present in a scene.

Biased Competition Theory of Visual Attention

One influential account of visual selective attention has been termed the biased competition theory (Beck & Kastner, 2009; Desimone & Duncan, 1995; Duncan, 2005). According to this theory, when multiple objects are present in a visual scene, they must compete for representation because the limited capacity of the visual system does not allow every item to be fully represented simultaneously (see also Tsotsos, 1990). In addition, the visual system exhibits selectivity such that we can process some objects at

the expense of others. This selectivity is achieved through bottom-up and top-down biasing signals. Objects that are salient or goal-relevant are selected and receive enhanced processing relative to less-salient or irrelevant objects. The biased competition model defines visual selective attention as an emergent property of competition for representation and its resolution through bottom-up and top-down influences (Desimone & Duncan, 1995).

Competitive Interactions

The first assertion of the biased competition theory is that objects compete for representation in the visual system. These mutually suppressive competitive interactions between objects are thought to occur at the level of the receptive field (RF; Beck & Kastner, 2009). When multiple objects fall within the same RF of a visual neuron, the objects compete to control the response of that neuron. If a single neuron were to simultaneously represent multiple objects, it is possible that the properties of the objects would be conflated, resulting in illusory conjunctions (Robertson, 2003). To avoid such problems, ideally each neuron codes the visual properties of only a single object at any one time. In other words, representing multiple objects can result in ambiguity and thus, the objects compete to control the responses of neurons to resolve this ambiguity (Luck, Girelli, McDermott, & Ford, 1997). It is thought that the objects compete through mutually suppressive interactions (Beck & Kastner, 2009) until the selected item alone controls the response of the neuron. This is consistent with the idea that attention serves to "shrink" the receptive fields of neurons to include only the selected item and minimize the suppressive influences of the unselected items (Beck & Kastner, 2009; Moran & Desimone, 1985; see Figure 1).

Competition for representation is likely to occur in higher-order visual areas. This is due to the fact that extrastriate and inferotemporal neurons have large RFs compared to striate neurons. It has been estimated that V1 neurons have RFs of less than 1° but by area V4 the RFs are 3-8° (Smith, Singh, Williams, Greenlee, 2001) and can be over 20° in areas TE and TEO (Boussaoud, Desimone, & Ungerleider, 1991). The larger RFs in the extrastriate and inferotemporal cortex make it more likely for multiple objects to be located within the same RF of a neuron. In these visual areas, competition for representation is spatially mediated as a consequence of the fact that competition occurs at the level of the RF. Within a given visual area, there is minimal competition for representation when the distance between objects is large enough such that each object falls into separate pools of RFs. However, as the distance between objects decreases, the objects necessarily are located in more of the same RFs and thus compete for representation.

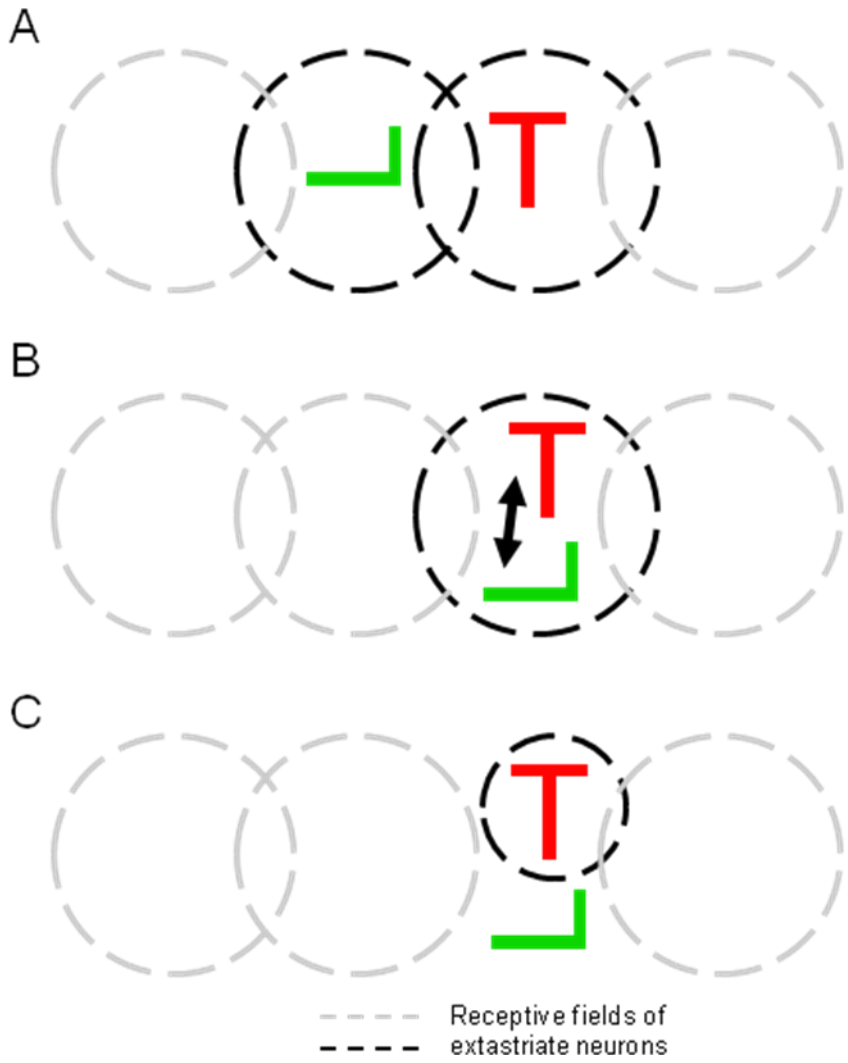

Figure 1. Diagram illustrating competition and selectivity in extrastriate cortex. (A) When the distance between stimuli is large enough that each falls into separate receptive fields (RFs), there is minimal competition for representation. (B) However, when two stimuli fall within a single RF, competition for representation occurs. Stimuli compete for representation through mutual suppression. (C) Eventually, one stimulus (the letter T) wins the competition for representation and the RF shrinks around the selected object.

Biasing the Competition: Bottom-up and Top-down Influences

The second important aspect of the biased competition account of visual selective attention is that the competition for representation can be biased toward certain objects based on both bottom-up and top-down factors. Bottom-up refers to purely stimulus-

driven factors that can bias processing towards salient objects in a visual scene. According to Desimone and Duncan (1995), bottom-up factors such as a local inhomogeneity or a sudden onset can bias the competition towards an object (c.f. "pop-out"; Treisman & Gormican, 1988). In other words, an object that is different from surrounding objects or an object that suddenly appears is particularly salient. For example, if there is a single red object among multiple green objects, the red item would be more salient than the green items. If there is competition among objects for representation, these bottom-up factors will bias processing towards the more salient items.

On the other hand, an individual can also bias competition in a top-down fashion. Top-down refers to factors that are inherent to the observer such as goal, knowledge, or expectations. These top-down factors can include knowledge of where a target is likely to appear or the features of the target object (Beck & Kastner, 2009; Desimone & Duncan, 1995). When the observer knows the features of a target object, they create an attentional template of the object. The attentional template is a short-term memory representation of behaviorally relevant object features (e.g., location, color, size, etc.; Desimone & Duncan, 1995). When an object matches the attentional template, the competition for representation is biased towards the matching object. For example, if you knew your friend was wearing a red hat, you would create an attentional template for the color red, a hat shape, and likely locations. This template would bias processing towards red objects at a certain height in the visual scene as you searched for your friend in the crowd.

Behavioral Evidence for Biased Competition

Behavioral evidence of competition for representation often comes from divided attention tasks. In general, it is more difficult to report the properties of two objects simultaneously compared to responding to a single object (Desimone & Duncan, 1995; Duncan, 1981; Duncan, 2005). In addition, it has been found that these competitive interactions can be spatially mediated. For example, Bahcall and Kowler (1999) asked participants to report the identity of two spatially-cued letters from a circular array. They found that identification accuracy deteriorated as the target letters were brought closer together. In addition, using a redundant targets paradigm, McCarley, Mounts, and Kramer (2007) found that processing capacity available for a pair of targets decreased with decreased spatial separation between the redundant targets, which would be predicted if spatial proximity increased the proportion of RFs shared by the target letters. Taken together, behavioral evidence from divided attention tasks support the basic assertion that objects compete through mutually suppressive interactions and these competitive interactions interfere with task performance. Moreover, these mutually suppressive competitive interactions are greatest at the level of the RF of visual neurons.

In these tasks, the spatially mediated interference appears to be tied to the attentional demands of the task, and is not simply a consequence of sensory interactions. For instance, Bahcall and Kowler (1999) observed interference between two targets even when sensory differences used to cue the targets (i.e., color) were removed 500 ms prior to the target display, equating targets and fillers at a sensory level. Similarly, McCarley, Mounts, and Kramer (2004) only observed interference between two color-cued items when both had to be attended; spatial interference was not observed when the task

required attention to be allocated to only one of two colored items in a display. Thus, while in many respects these results appears to be similar to the more general phenomenon of crowding (e.g., Kyllingsbaek, Valla, Vanrie, & Bundesen, 2007; Pelli, Palomares, & Majaj, 2004), these divided attention tasks appears to reflect competition among attentionally salient items within a display, as opposed to competition among all possible items within a display.

Target-Decoy Paradigm

Additional behavioral studies that support the biased competition theory have used variants of the target-decoy paradigm (e.g., Mounts & Gavett, 2004; Mounts, McCarley, & Terech, 2007). In the target-decoy paradigm, two objects – the target and the decoy – are presented among a circular array of filler objects. The strength of competition for representation between the two objects can be manipulated by varying the distance between the target and the decoy. In one variant, the target and decoy are color singletons presented among an array of gray distractors (see Figure 2). In this example, the target is orange or green and the decoy is always the opposite color. Moreover, the color of the target is chosen randomly on each trial. The target is the letter "T" whereas the decoy is the letter "L" and participants are instructed to respond to the orientation of the target letter. Under these conditions, the participant can create an attentional template that includes the color features orange or green and the form features for intersecting lines that make the letter "T". Presumably, the target and decoy are initially processed due to bottom-up salience because they are both colored objects among an array of gray filler objects. This initial processing may also be influenced by top-down biasing because both the target and the decoy have potential target features

(i.e., they are orange or green). However, only the target has the form features in the correct configuration to match the attentional template. Thus, eventually the decoy representation is suppressed because the decoy does not have the form features in the correct configuration.

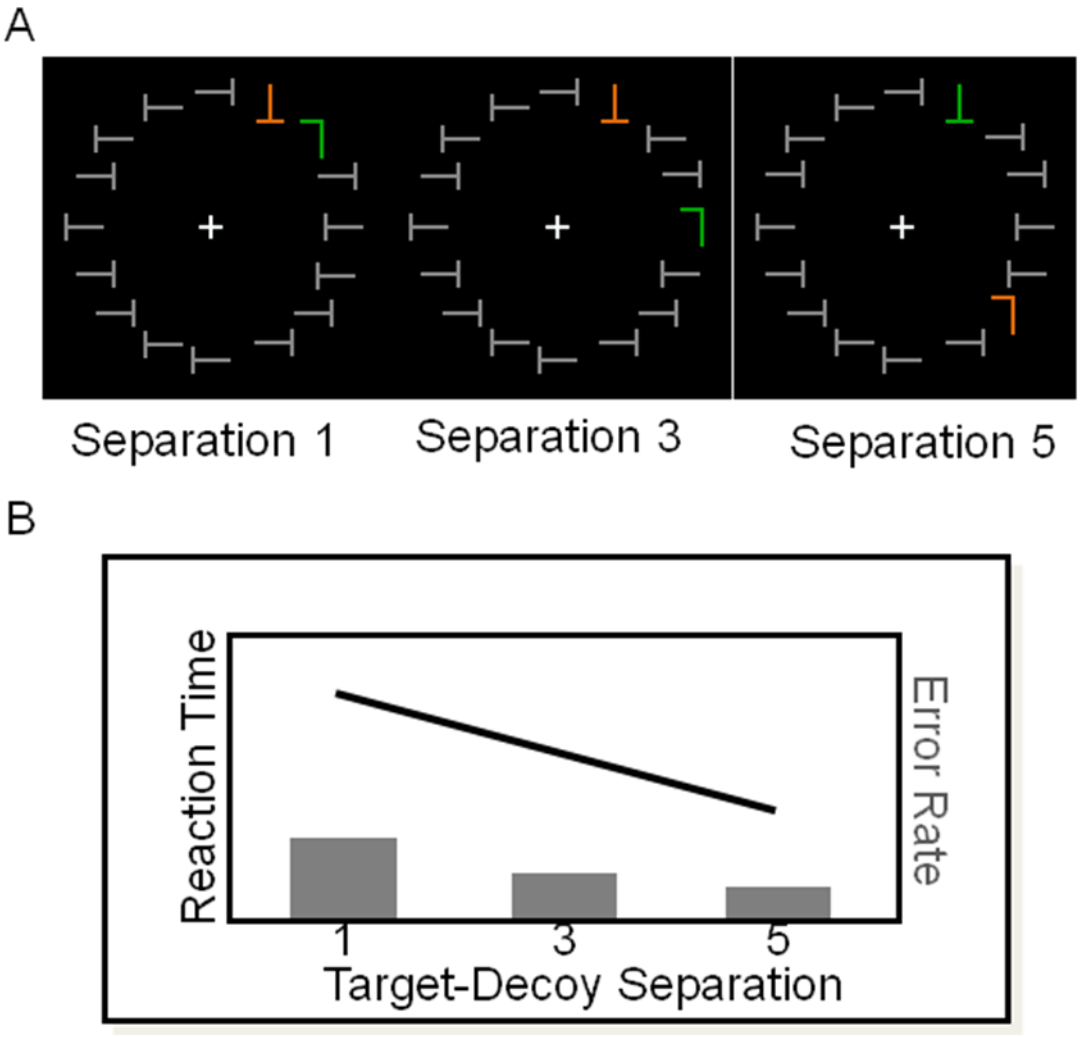

Figure 2. Example of a target-decoy paradigm and typical results. (A) Two color singletons – a target and a decoy – are presented among gray filler objects. In this example, the target is orange or green and the decoy is the opposite color. Participants respond to the orientation of the target (the letter "T") while ignoring the decoy (the letter "L"). The separation between the target and decoy is manipulated to vary spatially manipulated competition for representation. (B) Typically, participants are slower and less accurate when the target and decoy are near each other compared to when they are far apart. This is consistent with the idea that, as the two objects are presented closer together, they progressively fall into more overlapping receptive fields which increases competition for representation and degrades task performance.

Bottom-up and Top-down Influences

In a demonstration of bottom-up influence on attentional selection, Mounts and Gavett (2004) used a variant of the target-decoy paradigm. They presented a circular display of letters and cued two of the letters, the target and a decoy, and participants responded to the orientation of the target. Thus, in this version of the paradigm, the target and decoy were defined by spatial precues rather than their color. Critically, Mounts and Gavett manipulated the relative salience of the target and the decoy by varying the luminance of the cued letters such that the target or decoy could be brighter than the other. They found that performance accuracy was better when the target was relatively more salient than the nearby decoy. This is consistent with the idea that when the target was brighter than the decoy, processing was biased towards the salient target which enhanced performance. On the other hand, when the decoy was brighter than the target, processing was biased towards the salient decoy which slowed performance and caused errors.

In a demonstration of top-down influence on attentional selection, Mounts, McCarley, and Terech (2007) again utilized a variant of the target-decoy paradigm. They presented two color singletons – the target and the decoy – among an array of gray distractors. The similarity of the target and decoy was manipulated; the target was the letter "T" whereas the decoy could be the letter "L" or the letter "C". Reaction time was slowed and error rates increased when the decoy was more similar to the target. This is consistent with the idea that participants formed an attentional template containing the form features of the target letter and this created a top-down influence that biased processing towards objects that shared features with the attentional template. Therefore,

performance was better when the salient distractor did not share features with the attentional template because processing was biased towards the target only. On the other hand, performance decreased when the target and decoy were similar because the decoy shared some features with the attentional template and processing was biased towards both the target and decoy objects.

Physiological Evidence for Biased Competition in Nonhuman Primates

Several single-cell studies in monkeys have provided evidence for the first assertion of biased competition theory; objects compete for representation through mutually suppressive interactions (Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985; Reynolds & Desimone, 2003; Rolls & Tovee, 1995). For example, Reynolds, Chelazzi, and Desimone (1999) presented two behaviorally irrelevant stimuli to the RF of a recorded V2 or V4 extrastriate neuron. One object was preferred by the neuron (i.e., it produced a robust response when presented alone within the RF of the neuron), whereas the other object was non-preferred (i.e., it produced a minimal response when presented alone). When the two objects were presented together in the RF, the neuron's response was less than the sum of the response to the two objects when presented alone. This finding is taken as evidence that, when multiple stimuli are present in the RF of a single neuron, the stimuli compete through mutually suppressive interactions to control the response of that neuron. Several other studies have corroborated this basic finding in others areas such as IT (Chelazzi, Duncan, Miller, & Desimone, 1998; Miller, Gochin, & Gross, 1993) and MT (Britten & Heuer, 1999; Recanzone, Wurtz, & Schwarz, 1997). These studies provide evidence in favor of the

basic idea that multiple stimuli must compete for representation in the visual system due to capacity limits at the level of the RF.

Bottom-up biasing has been demonstrated in a single-cell study by varying the relative salience of two objects within the RF of an extrastriate neuron. To manipulate relative salience, Reynolds and Desimone (2003) varied the brightness of objects presented to the RFs of neurons. When a bright object was presented alone within the RF of the neuron, this bright object produced a robust response. However, when they added a second bright object, the response of the neuron was reduced, demonstrating competition for representation between the equally salient objects. Critically, when they reduced the brightness of the second object, the neuron's response increased. This is consistent with the idea that processing was biased towards the bright object which then dominated the neural response.

Single-cell studies have also demonstrated the influence of top-down biasing on competition for representation. Moran and Desimone (1985) recorded from extrastriate neurons while simultaneously presenting one preferred and one non-preferred stimulus to the RF of the neuron. They found that extrastriate neurons fired less when the non-preferred stimulus was behaviorally relevant compared to when the preferred stimulus was relevant. That is, biasing the competition to the non-preferred item suppressed neuronal activity related to the preferred item. Other studies have corroborated this basic finding (e.g., Chelazzi, Duncan, Miller, & Desimone, 1998; Reynolds, Chelazzi & Desimone, 1999). The time-course of this top-down biasing has also been demonstrated. Chelazzi, Miller, Duncan, and Desimone (2001) showed that the neural response is dominated by the behaviorally relevant stimulus within 150-200 ms of the presentation of

the objects. Taken together, these studies are consistent with the idea that attention serves to "shrink" the receptive fields of neurons to include only the selected item and minimize the suppressive influences of the unselected items (Beck & Kastner, 2009). In other words, the neuron only receives inputs from lower level neurons that represent the selected item and the inputs from the lower level neurons that represent the unselected item are temporarily inhibited.

fMRI Evidence for Biased Competition

Competitive interactions have also been demonstrated in humans using functional magnetic resonance imaging (fMRI). Kastner and colleagues (1998) provided evidence of mutually suppressive interactions between competing items by presenting multiple objects either simultaneously or sequentially and measured the BOLD-response in extrastriate and inferotemporal cortex. They found that the BOLD-response was reduced in the simultaneous condition compared to the sequential condition, indicative of mutually-suppressive competitive interactions when the objects were presented simultaneously. Kastner, De Weerd, Pinsk, Elizondo, Desimone, and Ungerleider (2001) extended these findings by demonstrating that the competition for representation occurs at the level of the RF. When multiple objects were presented near each other (2º separation), there was evidence of competition in areas V2, V4, and TEO. In contrast, when the objects were presented farther apart (7º separation), competition was only shown in area TEO. This is likely due to the fact that only area TEO had RFs large enough to encompass multiple objects when they were far apart. Taken together, these studies provide evidence that objects compete for representation in the visual system due to capacity limits at the level of the RF.

Neurophysiological evidence for bottom-up influences on competition for representation in humans has also been revealed by fMRI. Beck and Kastner (2005) used a variant of the simultaneous vs. sequential paradigm and measured the BOLD-response in extrastriate cortex. In one condition, all of the objects differed from the others, and therefore, none of the objects "popped out" from the surrounding objects. In another condition, a single object differed from the others in terms of color and orientation. Thus, this object was a local inhomogeneity and "popped out" from the surrounding objects. The results showed that the BOLD-response was similar for the simultaneous and sequential conditions when one object "popped out" from the surroundings whereas the BOLD-response was reduced in the simultaneous condition compared to the sequential condition when none of the objects "popped out". These results are consistent with the idea that processing was biased towards the "pop out" object due to its bottom-up salience.

Top-down biasing has also been demonstrated in humans using fMRI. Kastner and colleagues (1998) biased processing towards one object in a multi-object display by having participants perform a task on one of four objects based on location. They found that making one of the stimuli behaviorally relevant alleviated the reduction in BOLD signal that is usually observed when multiple objects are presented simultaneously. In other words, by biasing the competition towards one item, the suppressive influence of the other simultaneously presented items was reduced. Similar to the single-cell studies in monkeys, this result is consistent with the idea that attention serves to "shrink" the receptive fields of neurons to include only the selected item. It has also been demonstrated that the effect of top-down biasing scales with RF size. Bles, Schwarzbach,

De Weerd, Goebel, and Jansma (2006) varied the separation between simultaneously presented objects while participants performed a task on one object based on location. When the objects were close (2º separation), the effect of this top-down bias was seen in areas V2, V4, and TEO. Specifically, the top-down bias ameliorated the typical reduction of the BOLD signal due to competition for representation. However, when the objects were far apart (7º separation), the effect of the top-down bias could only be seen in area TEO where the RFs were large enough to incorporate multiple objects. These studies provide evidence that competition for representation in the visual system can be biased towards behaviorally relevant objects and this occurs at the level of the RF.

Interim Summary

The biased competition theory of visual selective attention has been well-supported by behavioral evidence and physiological evidence in both humans and nonhuman primates. I have presented evidence that supports the notion that when multiple objects are present in the visual scene, they compete for representation. Moreover, these competitive interactions are mutually suppressive and are greatest at the level of the RF. In addition, competition among objects for representation is biased towards objects based on both bottom-up and top-down factors. However, because the physiological evidence in humans presented thus far has been based on fMRI, there has been little neurophysiological evidence regarding the temporal dynamics of biased competition in humans. The event-related potential (ERP) technique is well-suited to provide critical information on the time-course of biased competition in the human visual system. Next, I will review evidence from lateralized ERPs that has given insight into the dynamics of biased competition in humans.

Lateralized Event-Related Potentials and Biased Competition

Lateralized ERPs are derived using the contralateral control method. In this section, first I will describe the contralateral control method in context of the ERP technique. Next, I will describe lateralized ERPs derived using the contralateral technique that have been used to examine visual selective attention. These lateralized ERPs include the N2pc, Ptc, and SPCN components. These components are thought to reflect the attentional selection of objects, the suppression of distractor information, and post-selection processing including representation in visual short-term memory (VSTM), respectively. Finally, I will present evidence from lateralized ERP studies that reveal the temporal dynamics of biased competition in humans.

Contralateral Control Method

One problem with traditional ERP measures is that it is often difficult to attribute specific psychological processes to the ERP activity (Luck, 2005). On the other hand, the contralateral control method allows the isolation of brain activity that is systematically related to the experimental variables while removing activity that is not related to the variables of interest (Coles, 1989; Gratton, Coles, Sirevaag, Eriken, & Donchin, 1988; Gratton, Corballis, & Jain, 1997; Luck, 2005; see Gratton, 1998 for a review). Thus, by utilizing the contralateral control method, the problem of assigning psychological processes to components becomes more manageable (although it is still not always a trivial or straightforward task).

The contralateral control method is predicated on the hemispheric organization of the cortex. A well-known example is the contralateral organization of the motor cortex. For example, when an individual prepares a hand movement, brain activity is greater in

the hemisphere contralateral to the hand compared to the ipsilateral hemisphere. For example, if a left hand movement is prepared, there is more activity in the right motor cortex than the left motor cortex. This allows the calculation of a lateralized ERP known as the lateralized readiness potential (LRP) following the contralateral control method (see Figure 3). When a left hand movement is prepared, activity from a scalp electrode over the left motor cortex (i.e., the hemisphere ipsilateral to the hand) is subtracted from a homologous electrode over the right motor cortex (i.e., the hemisphere contralateral to the hand). The same subtraction of ipsilateral activity from contralateral activity is computed for conditions where a right hand movement is prepared. Finally, left and right hand conditions are averaged together. These calculations remove activity that is the same in both hemispheres (e.g., general levels of arousal) and activity that is always different between the two hemispheres (e.g., greater activity in the left hemisphere because it is specialized for language). This leaves only the brain activity that is systematically lateralized to one hemisphere or the other based on preparing a left or right hand movement. Thus, by implementing the contralateral control method and good experimental design, it is easier to relate brain activity to underlying psychological processes because many alternative explanations are removed (Gratton, 1998).

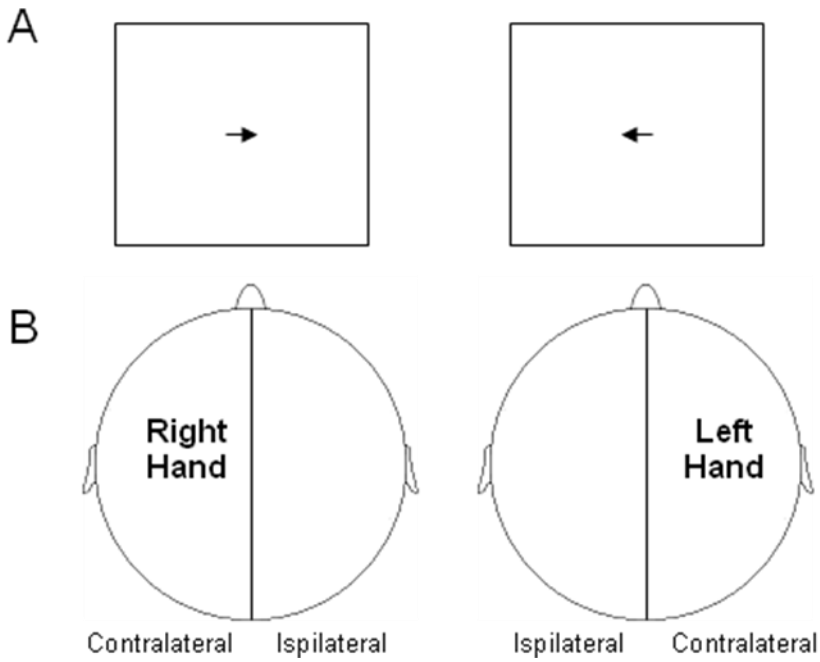

Figure 3. Diagram illustrating the contralateral control method. The contralateral control method derives the lateralized readiness potential (LRP) by subtracting the activity ipsilateral to the prepared hand movement from the activity contralateral to the prepared hand movement and then averaging over left and right hand movement conditions. (A) Cue that indicates whether the response will be executed with the right hand (right arrow) or with the left hand (left arrow). (B) Brain activation of the contralateral motor area in preparation of a right hand or left hand response.

The contralateral control method can be extended to measure lateralized potentials from other systems in the brain that also have a hemispheric organization such as the visual system. When utilizing the contralateral control method to measure lateralized ERPs from the visual system, there are some important methodological details that are necessary to isolate activity that is associated with attention rather than non-attentional sensory related processing. One crucial aspect is that the left and right visual fields should have equivalent sensory energy. Otherwise, differences in sensory energy between the two fields can cause differences in the contralateral and ipsilateral waveforms that will also influence the lateralized ERPs. For example, if there is one

bright object in the left visual field and no objects in the right visual field, it will be unclear whether the lateralized ERPs elicited by the object in the left visual field is due to attentional selection of the object or the fact that there is a sensory imbalance between the fields. Ideally, there should be identical sensory stimulation in both fields (Woodman & Luck, 2003b), but many studies have shown that balancing the luminance across fields is sufficient (Hickey, Di Lollo, & McDonald, 2009; Hilimire, Mounts, Parks, & Corballis, 2009; Sawaki & Luck, 2010). Using these strategies allows the isolation of lateralized ERPs that can be more directly related to attentional processes.

Lateralized ERPs that are thought to index the attentional selection of objects have typically been studied in the context of visual search paradigms. For example, a participant is presented with an array that contains multiple objects and the participant is asked to respond when a target stimulus is present in the array. As mentioned previously, it is critical for the contralateral control method that the sensory information is balanced across fields. For this reason, the search displays are generally bilateral with the number and luminance of objects equated across fields. By measuring activity after the onset of the visual search array, it is possible to use the contralateral control method to isolate lateralized ERPs that are thought to reflect processes involved in the attentional selection of the target object and the suppression of distractor objects.

Electrophysiological studies examining attentional selection in visual search have often examined the lateralized N2pc component (see Figure 4) as a dependent measure. The N2pc (N2-posterior-contralateral) is named for its latency range and scalp distribution (Luck & Hillyard, 1994a; 1994b). The N2pc occurs during the time window of the *N2* wave (175-250 ms after the onset of the target array) and is defined as more

negative voltage at *posterior* scalp sites *contralateral* to the attended object relative to corresponding ipsilateral scalp sites (Luck & Hillyard, 1994a; 1994b; see also Heinze, Luck, Mangun, & Hillyard, 1990; Luck, Fan, & Hillyard, 1993; Luck, Heinze, Mangun, & Hillyard, 1990; Luck & Hillyard, 1990). The N2pc component typically has its peak amplitude at scalp electrodes PO7/8 and P7/8 (Praamstra & Kourtis, 2010) which are located on the scalp over occipitotemporal cortex. The N2pc has been localized to the occipitotemporal cortex using EEG, MEG, and fMRI techniques (Hopf et al., 2000; 2002; 2006). Finally, the N2pc component is thought to index attentional selection processes including enhancement of target features and suppression of distractor representations.

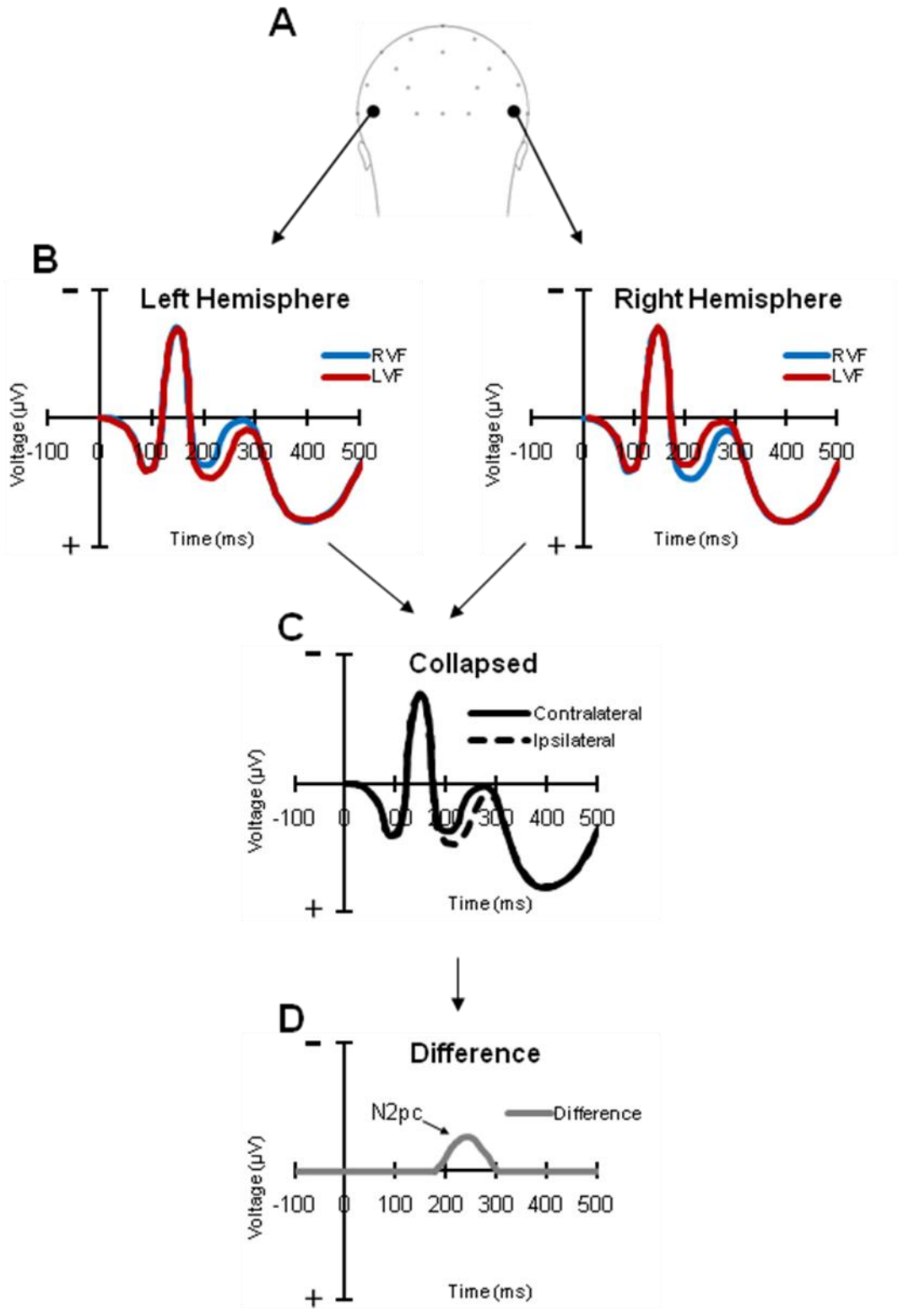
A
B
Left Hemisphere
RVF
LVF
Voltage (μV)
-100 0 100 200 300 400 500
Time (ms)
Right Hemisphere
RVF
LVF
Voltage (μV)
-100 0 100 200 300 400 500
Time (ms)
C
Collapsed
Contralateral
Ipsilateral
Voltage (μV)
-100 0 100 200 300 400 500
Time (ms)
D
Difference
N2pc
Difference
Voltage (μV)
-100 0 100 200 300 400 500
Time (ms)

Figure 4. Diagram illustrating the derivation of the N2pc component. (A) The N2pc component is maximal at occipitotemporal scalp sites. (B) In the left hemisphere, the ERPs are more negative when attention is directed to the right visual field (RVF) compared to the left visual field (LVF). In contrast, in the right hemisphere the ERPs are more negative when attention is directed to the LVF compared to the RVF. (C) To form the collapsed waveforms, the ipsilateral waveform is calculated as the average of the left hemisphere waveform when attention is directed to the LVF and the right hemisphere waveform when attention is directed to the RVF. The contralateral waveform is calculated as the average of the left hemisphere waveform when attention is directed to the RVF and the right hemisphere waveform when attention is directed to the LVF. (D) The N2pc component is calculated by subtracting the ipsilateral waveform from the contralateral waveform.

Temporal Dynamics of Biased Competition

Several studies have utilized the contralateral control method to examine competition for representation in the visual system. These studies have manipulated competition by varying the distance between a target and a distractor object(s) based on the idea that competition is spatially mediated. For example, Luck and colleagues (1997) compared the N2pc elicited by a single target with to the N2pc elicited by a target flanked by a nearby distractor. They found that N2pc amplitude increased when the target was presented with the nearby distractor compared to when the target was presented alone. Luck and colleagues suggested that this increase in N2pc amplitude indicates suppression of the nearby distractor. However, it is likely that the difference in N2pc amplitude shown by Luck and colleagues is actually due to the difference in the number of stimuli present in the two conditions. Thus, the results of Luck and colleagues (1997) cannot be interpreted as a reflection of competition in the visual system.

Mazza, Turatto, and Caramazza (2009) pointed out this confound evident in Luck and colleagues (1997) manipulation. Specifically, Luck and colleagues (1997) confounded distractor numerosity with distractor proximity. Mazza and colleagues (2009) held the number of distractors constant while varying the distance between a target and these distractors. They found that N2pc amplitude did not vary with the distance between

the target and distractors. However, the lack of N2pc modulation found by Mazza and colleagues (2009) is possibly due to the magnitude of the manipulation of separation between the target and the distractors. The distance between target and distractors only varied 1° of visual angle between conditions. Thus, it is possible that greater variation in the distance between the target and distractor objects would yield evidence for competition in the visual system.

My colleagues and I addressed this issue by utilizing a variant of the target-decoy paradigm described above. We manipulated the distance between the target and the decoy and measured the N2pc elicited by these salient color singletons (Hilimire, Mounts, Parks, & Corballis, 2009). The color of the target and decoy varied from trial to trial so that participants had to first determine which colored object was the target and then report the orientation of the target. Importantly, we varied the separation between the two objects over a larger range so that the distance between objects could be 2°, 6°, or 10° of visual angle. We found that participants were slower and committed more errors when the target and decoy were adjacent and the interference decreased as the distance between the target and decoy increased, indicating that spatially mediated competition for representation occurred. Corresponding to the behavioral data, N2pc amplitude was smallest when the target and decoy were adjacent and was greater in amplitude as the distance between the two attended items increased.

To ensure that these N2pc differences reflected attentionally-mediated competition and were not a consequence of low-level sensory interactions, we also had participants perform a localization task on the same stimulus configurations. Participants responded whether the two colored objects appeared to the left or right of fixation and the

results showed that N2pc amplitude did not vary with the separation between the two colored objects. Thus, the N2pc results did not reflect low-level sensory interactions, but rather indexed spatially mediated competition when the target had to be individuated in the orientation discrimination task. We concluded that the observed reduction in N2pc amplitude may reflect degraded target selection processes due to increased competition for representation between two spatially proximal objects.

Our results also revealed another component that occurred after the N2pc. We called this additional component the Ptc because it is a *positivity* that was found to be distributed more towards the *temporal* electrodes (compared to the more posterior N2pc component) *contralateral* to attended objects (Hilimire, et al., 2009). The Ptc component occurs at approximately 275-340 ms post-stimulus and its amplitude increased with decreasing target–decoy separation. After the two colored items are initially processed, the Ptc may reflect suppression of the distractor representation that is necessary to resolve the competition between the two salient color singletons.

Because the Ptc was a novel component that had not been previously quantified, we conducted a follow-up study to examine a remaining question regarding the functional significance of the Ptc component in relation to competition for representation in the visual system (Hilimire, Mounts, Parks, & Corballis, 2010). Previously, we had found that the Ptc component increased in amplitude when the N2pc decreased in amplitude (and vice versa) which may suggest that the Ptc component simply reflects persistent N2pc activity rather than a distinct component that indexes distinct attentional mechanisms. To address this issue, we demonstrated that the N2pc and Ptc components are at least partially dissociable and therefore are likely to reflect different aspects of

biased competition. In one experiment, we employed a same-different task to dissociate the N2pc component from the Ptc component. Participants responded to two targets by indicating whether they were same or different letters and the distance between the two targets was systematically manipulated. Under these conditions, the N2pc component varied with target-target separation but the Ptc did not. In another experiment, participants responded to the orientation of a target while ignoring a decoy. The distance between the target and decoy and the relative salience of the target and decoy were manipulated. The results demonstrated that the N2pc was sensitive to both the distance and relative salience manipulations while the Ptc was modulated by only the distance manipulation. These results indicate that the N2pc and Ptc components are sensitive to different variables and likely reflect distinct neural processes related to attentional selection.

Taken together (Hilimire et al., 2009; 2010), our results reveal the temporal dynamics of biased competition in humans. In the visual search tasks used in these studies, it is likely that both the target and decoy are processed initially due to their bottom-up salience. Next the decoy representation is suppressed and only the target receives continued processing to allow the discrimination of the target's orientation. Hilimire and colleagues (2009; 2010) found that an N2pc component was elicited by the salient objects (i.e., the target and decoy) and this likely reflects the initial processing of both the salient objects which occurs at approximately 175-250 ms after the onset of the objects. Moreover, this initial processing is degraded by the mutually suppressive competitive interactions between the objects (c.f., Beck & Kastner, 2009). After the initial processing of both salient objects, the target is identified and the decoy

representation can be suppressed. We have argued that the suppression of the decoy may be reflected by the Ptc component which occurs approximately 275-350 ms after the onset of the objects. Thus, by measuring lateralized ERPs, it is possible to observe how biased competition for representation unfolds over time in these tasks.

Lateralized ERP Indices of Target and Distractor Processing

The previous physiological evidence in humans has not addressed the degree to which competition and selectivity affects target and distractor processing. In the fMRI studies (e.g., Kastner et al., 1998), target and distractor objects are presented and the resulting BOLD-response can be driven by both target enhancement and/or distractor suppression. Similarly, with the previous lateralized ERP studies (Hilimire et al., 2009; 2010; Luck et al., 1997; Mazza et al., 2009) it was not possible to separate target related processing from distractor related processing. Because the target and distractor objects always appeared together in the left or right visual field, potential contributions of target and distractor processing were conflated in the lateralized N2pc and Ptc components. However, the contralateral control method can be adapted to examine target and distractor processing separately.

Hickey, Di Lollo, and McDonald (2009) developed a technique to examine distinct indices of target and distractor processing. They had participants view simple search arrays containing only one target and one distractor. In a large proportion of trials, one of two objects was presented on the vertical meridian of the display while the other was presented at a lateral location. Any lateralized activity in the ERP elicited in these trials could be unambiguously associated with the lateralized stimulus (see also Woodman & Luck, 2003b). When the target was lateralized and the distractor was on the

vertical meridian, Hickey and colleagues found that a negative component emerged over contralateral visual cortex, but that when the target was on the vertical meridian and distractor was lateralized, a positive contralateral component became apparent. The authors suggested that the target-elicited negative component - the *target negativity* (Nt) - reflected attentional modulation of target processing. In contrast, the distractor-elicited positive component –the *distractor positivity* (Pd) – appeared to index direct suppression of the distractor representation. Thus, utilizing a variant of their design, it is possible to measure ERP components that reflect target processing and distractor processing separately.

Recently, my colleagues and I (Hilimire, Mounts, Parks, & Corballis, 2011) adapted the target-decoy paradigm we used previously so that we could examine target and distractor related processing separately. As before, we presented participants with two salient objects – a target and a decoy – embedded in an array of gray filler objects. Critically, we placed either the target or the decoy on the vertical meridian while the other object was presented in the left or right visual field (c.f., Hickey et al., 2009). This way, only the lateral stimulus can contribute to a lateralized ERP component (Hickey et al., 2009; Woodman & Luck, 2003b). In addition to the N2pc and Ptc components, we also examined the lateralized SPCN (sustained posterior contralateral negativity) component to capture more of the dynamics of competition and its resolution. The SPCN occurs approximately 350 ms after the onset of the visual search array and is thought to reflect post-selection processing including representation of attentionally selected objects in visual short term memory (VSTM; Emrich, Al-Aidroos, Pratt, & Ferber, 2009; Robitaille & Jolicoeur, 2006).

The results revealed the dynamics of both target and decoy processing. First, an N2pc component was elicited by both the target and the decoy. This likely reflects the initial processing of both the salient objects. Next, we found that only the decoy elicited a Ptc component. After the initial processing of both salient objects, the target is identified and the decoy representation can be suppressed. The suppression of the decoy is reflected by the Ptc component. Whereas the decoy representation is suppressed, the target undergoes continued processing. Corresponding to this, only the target elicited an SPCN which reflects post-selection processing including the VSTM representation of the target. Thus, using this design, it is possible to examine target and distractor processing separately and how attentional selection evolves over time.

Dissertation Studies

The current studies utilized the contralateral control method to investigate the degree to which competition and selectivity in the visual system influences target and distractor processing. In Experiment 1, I manipulated competition for representation in a target-decoy paradigm and examined the effects of competitive interactions on lateralized ERP correlates of target and distractor processing. Specifically, I compared conditions where a target or decoy is presented alone among filler objects to conditions where both color singleton objects appear simultaneously and can compete for representation. Because visual selective attention is thought to operate on both targets and distractors (Hickey et al., 2009; for a review see Treue, 2001), it was hypothesized that this technique would reveal when and how competition for representation affects both target and distractor processing.

Another unanswered question is whether biasing the competition through top-down mechanisms affects target and/or distractor processing. Previous techniques have demonstrated effects of top-down biasing, but it was impossible to determine whether this affected target and/or distractor processing (e.g., Kastner et al., 1998). In Experiment 2, I introduced a top-down factor to bias the competition toward the target, and I examined the effects on target and distractor processing. Specifically, I used the target-decoy paradigm from Experiment 1, but I told participants the color of the target in advance so that the decoy can be more easily suppressed. Thus, the experiment investigated when and how this top-down bias manipulation affects target and/or distractor processing.

The final experiment addressed a potential low-level sensory explanation for the results obtained in Experiments 1 and 2. As discussed above, it is possible that imbalances in sensory energy between the two fields can influence the lateralized ERP components. In Experiment 1 and 2, there were colored object(s) in the left or right visual field, whereas there were only gray objects in the opposite visual field. It is possible that this imbalance lead to sensory related differences in the lateralized ERPs that were confounded with the attentional processes under investigation. Therefore, Experiment 3 was a control experiment that examined whether the lateralized ERP that were obtained in Experiments 1 and 2 are related to attention or are due to sensory imbalances in the displays. Participants were presented with the same displays as Experiment 1 except they now performed a difficult search task at fixation. This way, their attention was focused on fixation and should not have been deployed to the peripherally presented target or decoy. The logic of this control experiment was that if

there was no lateralized ERP activity under these conditions, then the lateralized ERPs from Experiment 1 and 2 reflect attentional processes. On the other hand, if there was still lateralized ERP activity elicited when attention was focused on fixation, then sensory imbalances were likely contributing to the lateralized ERPs, and consequently the results from Experiments 1 and 2 would have to be interpreted with caution.

CHAPTER 2

EXPERIMENT 1

In Experiment 1, I examined the degree to which competition and selectivity in the visual system influences target and distractor processing. Using a variant of the target-decoy paradigm used previously (Hilimire et al., 2011), I placed either the target or the decoy in the left or right visual field while the other object (if present) was placed on the vertical meridian. Again, only the lateral stimulus can contribute to a lateralized component such as the N2pc, Ptc, and SPCN components. I manipulated competition by presenting the target or decoy alone or presenting the target and decoy together. This way, it was possible to examine whether competition affects target processing, distractor processing, or both.

It was hypothesized that both the target and decoy would elicit an N2pc component that would vary in amplitude with the competition manipulation. This would reflect that both the target and decoy are initially processed, and that competition can degrade processing of both attended objects. In addition, it was hypothesized that only the decoy would elicit a Ptc component based on previous results (Hilimire et al., 2011). Moreover, it was hypothesized that Ptc amplitude would vary with the competition manipulation indicating increased distractor suppression with increased competition (Hilimire et al., 2009; 2010). Finally, it was hypothesized that only the target would elicit an SPCN component which would reflect that only the target receives post-selection processing including representation in VSTM (Hilimire et al., 2011), but it is unclear how the competition manipulation will affect the SPCN component.

Method

Participants

16 undergraduate students (aged 18-28 years, M = 20.4 years, SD = 2.7 years) participated for course credit. All participants had normal or corrected-to-normal vision, assessed by self-report. In addition, all participants had normal red-green color vision, assessed by the Ishihara color test. All participants gave written, informed consent prior to beginning experimentation, and all research was approved by the institutional review board at Georgia Institute of Technology.

Stimuli and Design

The stimulus displays (see Figure 5 for example displays) consisted of 16 letters (Ts and Ls; 1.2° x 1.2°) arranged in equal intervals around an imaginary circle with a radius of 6° of visual angle centered on fixation (gray point; 0.3° x 0.3°). The displays were presented on a uniform black background. Fourteen or fifteen (depending on the condition) of the letters were 'filler' items which were gray (x = 0.26, y = 0.27, Y = 1.2) Ts that are randomly rotated 90° to the left or right. The remaining one or two items (depending on the condition) were colored letters: the 'target' and the 'decoy'. The target was an upright or inverted T that was colored either orange (x = 0.42, y = 0.41, Y = 1.2) or green (x = 0.22, y = 0.35, Y = 1.2). The color of the target was chosen randomly on each trial. The decoy was an upright or inverted L that was also colored either orange or green but was the opposite color of the target. Four of the objects appeared on the meridians and there were three objects in each visual quadrant. In addition, four gray squares (0.25º x 0.25º, x = 0.26, y = 0.27, Y = 1.3) were included in the display, each

centered 0.25º diagonally from the fixation point. Three of the squares had a gap (0.25º) on the right or left side, and one square had a gap on the top or bottom.

In the first condition (target alone condition), the target was presented in one of the positions adjacent to the horizontal meridian to obtain ERPs related to target processing in absence of competition from the decoy. In the second condition (decoy alone condition), the decoy was presented adjacent to the horizontal meridian to obtain ERPs related to decoy processing in absence of competition from the target. In the third condition (together, lateral target condition), the target was presented adjacent to the horizontal meridian while the decoy was presented on the vertical meridian in the same visual quadrant to obtain ERPs related to target processing in the presence of competition. Finally, in the fourth condition (together, lateral decoy condition), the decoy was presented adjacent to the horizontal meridian while the target was presented on the vertical meridian in the same visual quadrant to obtain ERPs related to decoy processing in presence of competition.

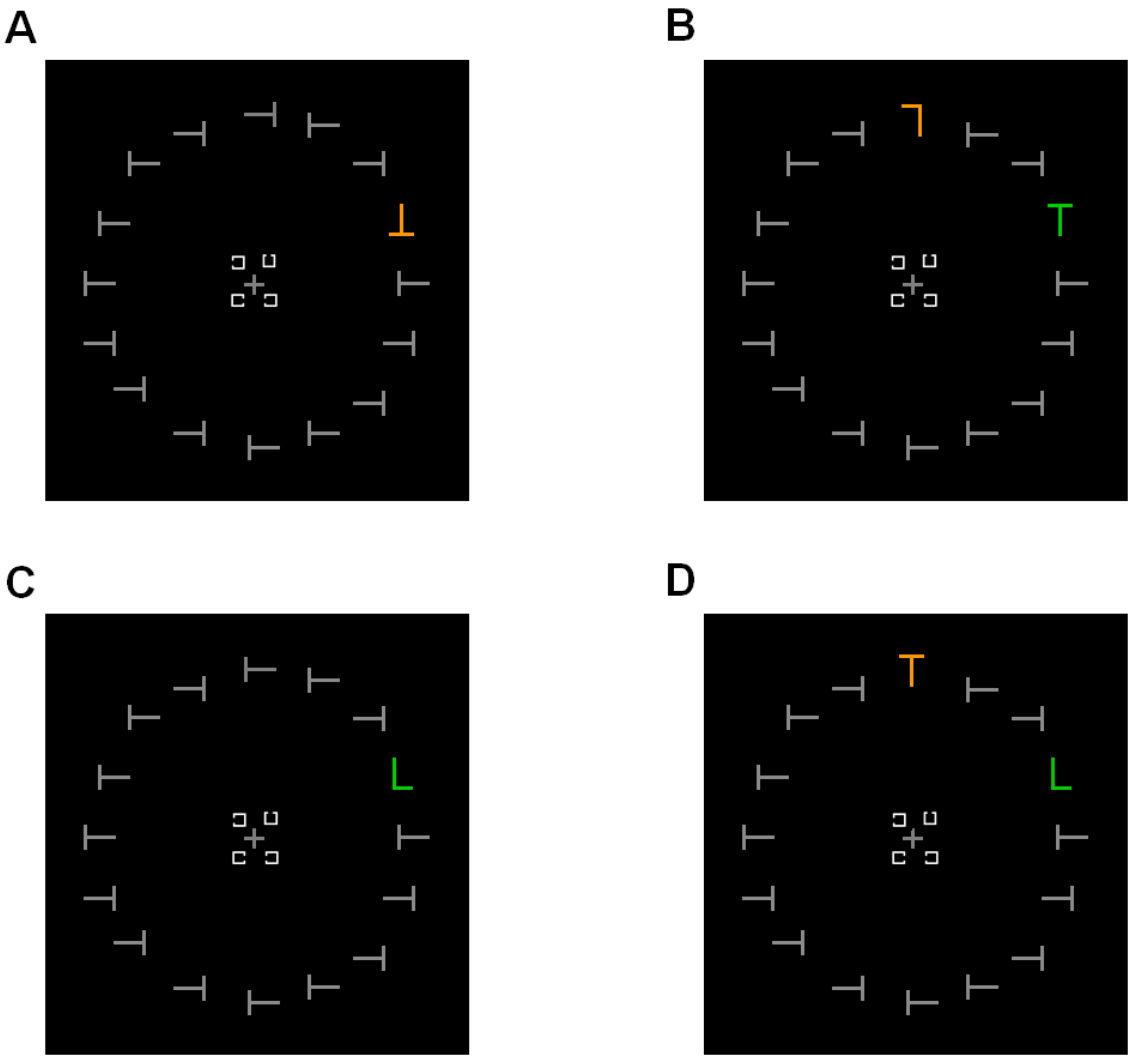

Figure 5. Examples of the stimulus displays used in all three experiments. The target (colored letter T) and the decoy (colored letter L) are presented among gray filler objects. (A) Target alone condition. The target is displayed alone in a lateral position to elicit lateralized ERPs associated with target processing with minimal competition. (B) Target and decoy together condition. The target is displayed in a lateral position and the decoy is on the vertical meridian to elicit lateralized ERPs associated with target processing when there is competition between the target and decoy. (C) Decoy alone condition. The decoy is displayed alone in a lateral position to elicit lateralized ERPs associated with decoy processing with minimal competition. (D) Decoy and target together condition. The decoy is displayed in a lateral position and the target is on the vertical meridian to elicit lateralized ERPs associated with decoy processing when there is competition between the decoy and target.

Procedure

Participants were seated in a darkened, sound-attenuating booth. Experimental stimuli were presented on a 21-inch CRT monitor positioned 57 cm from the participant with viewing distance maintained through the use of a chinrest. The participants were instructed to report the orientation of the target as quickly as possible (when it was present) while maintaining approximately 90% accuracy. Participants were instructed to withhold their response if no target was present. Responses were given using the number pad of a standard keyboard using the right hand ('1' for an inverted T with right index finger, '2' for an upright T with right middle finger). A trial began with the presentation of the fixation point and the duration was drawn from an approximately exponential distribution ranging from 500 - 2000 ms. The stimulus array was flashed for 200 ms and the fixation point remained until a response was given. Incorrect responses were signaled by an 'X' displayed at the center of the screen. Participants completed 24 practice trials followed by 24 blocks of 48 experimental trials each for a total of 1152 trials. The order of trials was randomized within each block.

Electrophysiological Recording and Analysis

Electrophysiological data was recorded using a Biosemi ActiveTwo amplifier system (Amsterdam, Netherlands). Scalp potentials were recorded from 32 electrodes: FP1/FP2, AF3/4, FC1/2, FC5/6, F7/8, F3/4, Fz, C3/4, Cz, CP1/2, CP5/6, P7/8, PO3/4, P3/4, Pz, T7/8, O1/2, and Oz. Two additional electrodes were placed on the mastoids. The ActiveTwo system required the placement of two additional electrodes: common mode sense (CMS) and driven right leg (DRL). The electroencephalogram (EEG) was digitized at 512 Hz and was acquired with respect to the CMS electrode.

EEG data was analyzed using BrainVision Analyzer (Brain Products, Gilching, Germany). Offline, all channels were re-referenced to the algebraic average of the left and right mastoids. Electrooculogram (EOG) was calculated offline as the difference between electrodes positioned above and below the left eye and on the outer canthi of each eye for vertical electrooculogram (VEOG) and horizontal electrooculogram (HEOG), respectively. Continuous EEG was digitally band-pass filtered from 0.1 to 30 Hz using a zero phase-shift Butterworth filter (12 dB/oct). EEG was segmented into 600 ms segments beginning 100 ms pre-stimulus and continuing 500 ms post-stimulus. Segments were baseline corrected by setting the average of the 100 ms pre-stimulus baseline to zero. Segments containing activity greater than ±100 μV in the scalp channels and/or activity greater than ±60 μV in the VEOG channel were considered artifacts and rejected. Additionally, a two-step procedure to exclude eye-movements was implemented. First, any segments with activity greater than ±25 μV in the HEOG channel were considered artifacts and rejected. Next, participants' averages were formed for right and left visual field targets separately. Participants were replaced if their average remaining HEOG activity exceeded ±3.2 μV (7 participants were replaced). The grand average HEOG of the participants included in the analysis did not exceed ±2.0 μV.

Participant averages were formed separately for lateral targets and lateral decoys at each level of competition (alone vs. together). Difference waveforms were computed by subtracting activity at ipisilateral electrodes from activity in the corresponding contrlateral electrode. Grand average waveforms were formed from the participant averages in each condition.

ERP components were quantified from the contralateral minus ipsilateral difference waveforms separately for each level of object type (target vs. decoy) and competition (alone vs. together). The components were quantified using a peak measure that included ±20 data points around the peak which provides the mean activity in an approximately 41 ms time window centered at the individual's average peak for each condition. The peak measures were quantified at electrodes PO3/4 and P7/8. A preliminary analysis found no differences between the electrodes. Thus, activity at PO3/4 and P7/8 was averaged to obtain the dependent measure.

For statistical analysis, a repeated-measures ANOVA with object type (target vs. decoy) and competition (alone vs. together) as within-subjects factors was computed for each ERP component. In addition, to follow up on significant ANOVA effects, one-sample *t*-tests were performed comparing the peak activity to 0 μV to establish whether there was a reliable ERP component elicited in each condition.

Results

Participants were slower when the target and decoy were presented together (M = 518.95 ms, SD = 103.92 ms) compared to when the target was presented alone (M = 445.42 ms, SD = 101.92 ms), $t(15) = 10.59$, $p < 0.01$. In addition, proportion correct was reduced when the target and decoy were presented together ($M = 0.95$, $SD = 0.03$) compared to when the target was presented alone ($M = 0.97$, $SD = 0.02$), $t(15) = 4.06$, $p < 0.01$.

Figure 6 displays the contralateral-ipsilateral difference waveforms and Figure 7 shows the scalp topographies of the N2pc, Ptc, and SPCN components obtained in Experiment 1. As can be seen in Figures 6 and 7, both the lateral target and lateral decoy

elicited an N2pc component. Moreover, N2pc amplitude is reduced in the together conditioned compared to the alone condition. This was confirmed with a main effect of competition, $F(1,15) = 20.92$, $p < 0.01$, $\eta_p^2 = 0.58$. The main effect of object type, $F(1,15) = 1.09$, $p = 0.31$, $\eta_p^2 = 0.07$, and the interaction ($F < 1$) were not statistically significant. The one-sample *t*-tests revealed that a significant N2pc was elicited in each condition: lateral target alone, $t(15) = -5.72$, $p < 0.01$; lateral target with decoy, $t(15) = -5.80$, $p < 0.01$; lateral decoy alone, $t(15) = -5.25$, $p < 0.01$; lateral decoy with target, $t(15) = -3.75$, $p < 0.01$.

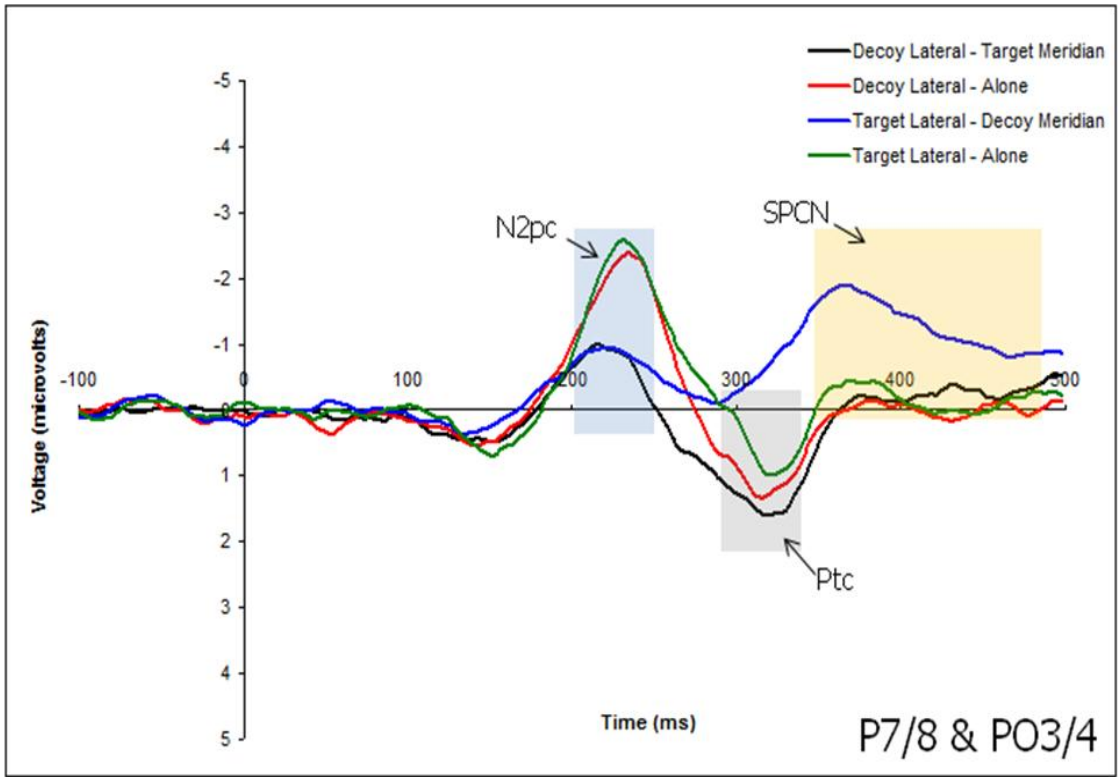

Figure 6. Contralateral minus ipsilateral difference waveforms for Experiment 1. These difference waveforms were calculated by subtracting the waveforms ipsilateral to the target and decoy from the waveforms contralateral to the target and decoy. Both the target and decoy elicit an N2pc component and the amplitude of the N2pc component is reduced for the together compared to the alone condition for both the target and the decoy. A Ptc component is evident in both decoy conditions. Finally, only the target when presented together with the decoy elicits an SPCN component.

Visual inspection of Figures 6 and 7 reveals that the Ptc component is elicited most strongly by the lateral decoy. Moreover, for the lateral decoy Ptc amplitude is greater when the target is also present. On the other hand, there is no Ptc activity for the lateral target alone, whereas when the decoy is present there is a small contalateral *negativity*. These observations were confirmed statistically; there was a main effect of object type, $F(1,15) = 31.87$, $p < 0.01$, $\eta_p^2 = 0.68$, which was qualified by a significant interaction between object type and competition, $F(1,15) = 5.97$, $p < 0.05$, $\eta_p^2 = 0.29$. The main effect of competition was not statistically significant ($F < 1$). One-sample *t*-tests revealed that when the lateral decoy was alone, $t(15) = 2.87$, $p < 0.05$, or presented together with the target, $t(15) = 5.61$, $p < 0.01$, a significant Ptc component was elicited. When the lateral target was presented alone, no significant Ptc component was elicited, $t(15) = 1.34$, $p = 0.20$. However, when the lateral target was presented with the decoy, a significant contralateral *negativity* persisted through the Ptc time window, $t(15) = -2.33$, $p < 0.05$. Thus, only the decoy elicited a Ptc which increased with competition. On the other hand, the target elicited a contralateral negativity when presented with the decoy, and no significant activity when presented alone.

As can be seen in Figures 6 and 7, an SPCN component was only elicited in the condition where the lateral target was presented with the decoy. In confirmation of this observation, there was a main effect of object type, $F(1,15) = 13.81$, $p < 0.01$, $\eta_p^2 = 0.48$, and competition, $F(1,15) = 6.83$, $p < 0.05$, $\eta_p^2 = 0.31$, which were qualified by a statistically significant interaction, $F(1,15) = 5.22$, $p < 0.05$, $\eta_p^2 = 0.26$. Indeed, one-sample *t*-tests confirmed that only the lateral target presented with the decoy elicited a significant SPCN component, $t(15) = -6.27$, $p < 0.01$ (all other ts < 0.66, ps > 0.52).

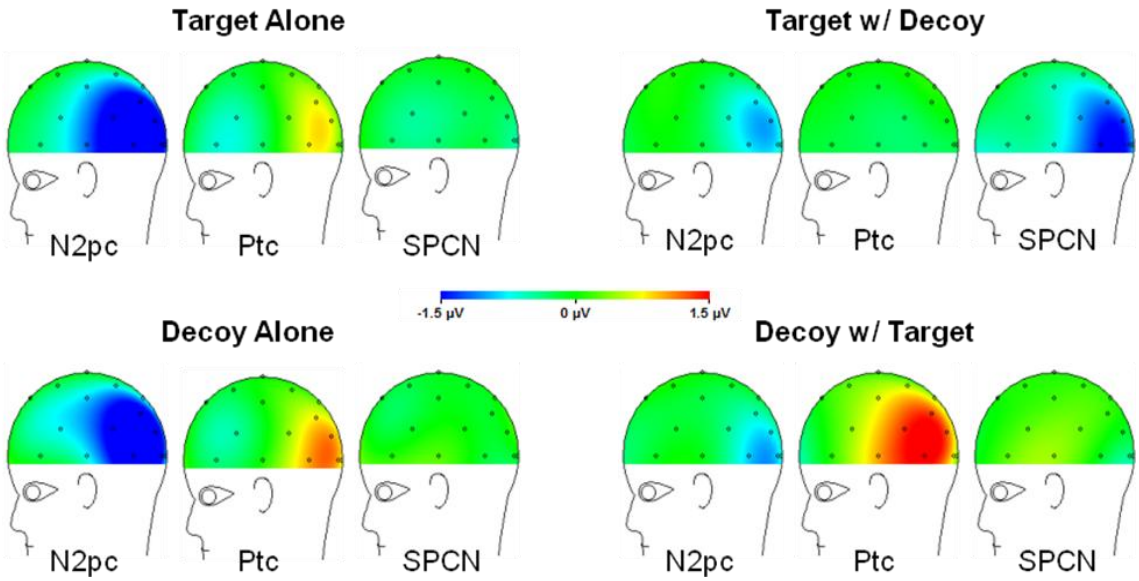

Figure 7. Scalp topographies for Experiment 1. The N2pc and SPCN component show their typical posterior topography over the contralateral scalp. The Ptc component is also distributed over the posterior scalp but is slightly more anterior than the N2pc and SPCN.

Discussion

Experiment 1 sought to investigate the degree to which competition affects target and distractor processing in visual search. Participants responded to the orientation of a target color singleton (a green or orange letter T) when it was present in the display, and ignored a decoy color singleton (letter L in the opposite color of the target) when it was present in the display. Participants did not know the color of the target in advance. Critically, the target or the decoy was presented in the left or right visual field while the other object, if present, was placed on the vertical meridian so that only the lateral stimulus would contribute to the lateralized ERP components (i.e., the N2pc, Ptc, and SPCN components). Competition between the objects was manipulated by presenting the target or decoy alone (less competition) or presenting the target and decoy together (more competition).

The N2pc results provide a nice extension of previous findings. The N2pc component was sensitive to competition for representation between salient objects. Specifically, both the target and decoy elicited an N2pc component, and N2pc amplitude was reduced when both singletons were present in the display compared to when only one singleton was present. This suggests that N2pc amplitude is reduced by the mutually suppressive competitive interactions between the objects. Importantly, this unambiguously demonstrates that competition for representation affects processing of both the task-relevant target and the task-irrelevant decoy.

These N2pc results extend the findings of Hilimire and colleagues (2009) to a different type of competition. In the previous experiments, Hilimire and colleagues manipulated competition for representation by varying the distance between the target and the decoy. N2pc amplitude was smallest when the target and decoy were adjacent, and was greater in amplitude as the distance between the two attended items increased. Thus, competition induced by varying the distance between the objects, and competition induced by varying the presence or absence of the second color singleton both reduce N2pc amplitude. This suggests that both types of competition degrade attentional selection processes as indexed by reduced N2pc amplitude.

Activity in the Ptc interval was similar to previous experiments. Experiment 1 results show that the Ptc component elicited by the decoy increased in amplitude with increased competition. Previously, Hilimire and colleagues (2009; 2010) also showed that Ptc amplitude increases with competition when competition is manipulated via the distance between the target and decoy presented together in the same visual field. In Experiment 1, there was no significant activity in this interval for the lateral target

presented alone, whereas there was a contralateral negativity when the target competed with the decoy. This contralateral negativity may be the early onset of SPCN activity in this condition. Overall, the contralateral positivity which I have been calling the Ptc component seems to be linked to distractors, and increases in amplitude with increased competition between the color singletons.

The SPCN results extend previous findings by showing that the SPCN is sensitive to competition. Previously, Hilimire and colleagues (2011) showed that only the target elicited an SPCN. Here, in Experiment 1, again only the target elicited an SPCN. Critically, however, the target did not elicit an SPCN component when presented alone, but rather only when it was in competition with the decoy. This suggests that the additional processing indexed by the SPCN is only necessary when there is competition between the target and decoy.

The time-course of competition and selectivity revealed by the lateralized ERP components analyzed here fits well with a previous examination of the time-course of attentional selection. Boehler, Tsotsos, Schoenfeld, Heinze, and Hopf (2009) presented a target surrounded by distractors. After the imperative display, they presented a probe at the target or distractor locations and measured the MEG response to the probe. Critically, they varied the stimulus onset asynchrony (SOA) between the display and the probe. They found that the event-related magnetic field (ERMF) elicited by the probe varied as a function of both the probe location and the SOA. First, they found that the ERMF was reduced at distractor locations adjacent to the target when the probe was presented 250 ms after the search display. This roughly corresponds to the onset of the Ptc component measured in Experiment 1. Next, they found that the ERMF was enhanced at the target

location when the probe was presented 325 ms after the search display. This roughly corresponds to the onset of the SPCN component measured in Experiment 1. Taken together, this suggests that the Ptc component might be linked to suppression of the decoy or disengagement of decoy processing in Experiment 1. The SPCN then might reflect target enhancement that occurs when the suppressive influence of the decoy is eliminated.

CHAPTER 3

EXPERIMENT 2

In the target-decoy paradigm as it has been used previously (Hilimire et al., 2009; 2010; 2011; Experiment 1), the participant does not know which color the target and decoy will be before the trial begins, and the target object is defined by its form alone. In Experiment 2, I told the participants the color of the target before the experiment so that the participant could also differentiate the target from the decoy based on color. Otherwise, the experiment was identical to Experiment 1. The hypothesis was that this top-down influence (i.e., knowledge of the color of the target) should help alleviate some of the competition for representation between the target and decoy, and may alter the dynamics of the competition and its resolution.

For example, for some participants the color of the target will always be green. Presumably, under these conditions the participant can create an attentional template that includes the color feature green and the form features for intersecting lines that make the letter "T". Due to bottom-up factors, both the target and decoy are still salient because they are colored objects amongst an array of gray filler objects. However, now only the target matches the color feature in the attentional template. This has a potential to reduce the competition between the target and the decoy because the competition can be more easily biased to the target since its color is known beforehand. In addition, there is the potential to suppress the decoy earlier in processing. Thus, Experiment 2 examined the effect of this additional top-down information on the temporal dynamics of biased competition.

Method

The method was similar to Experiment 1 with the following changes.

Participants

16 undergraduate students (aged 18-29 years, M = 19.9 years, SD = 2.6 years) participated for course credit.

Stimuli and Design

The stimulus displays were identical to Experiment 1 except that the target color was fixed.

Procedure

The procedure was identical to Experiment 1 except that participants knew the color of the target. For half the participants, the target was orange, and for the other half of the participants, the target was green. The decoy was always the opposite color of the target.

Electrophysiological Recording and Analysis

Recording and analysis was identical to Experiment 1. Participants were replaced if their average remaining HEOG activity exceeded ±3.2 μV (2 participants were replaced). The grand average HEOG of the participants included in the analysis did not exceed ±2.0 μV.

Results

Participants were slower when the target and decoy were presented together (*M* = 438.42 ms, *SD* = 102.55 ms) compared to when the target was presented alone (*M* =

425.86 ms, *SD* = 100.22 ms), $t(15) = 4.56$, $p < 0.01$. In contrast, proportion correct was not significantly different when the target and decoy were presented together (*M* = 0.94, *SD* = 0.06) compared to when the target was presented alone (*M* = 0.94, *SD* = 0.07), $t(15) = 0.54$, $p = 0.06$.

Figure 8 displays the contralateral-ipsilateral difference waveforms and Figure 9 shows the scalp distributions of the N2pc, Ptc, and SPCN components obtained in Experiment 2. As can be seen in Figures 8 and 9, only the lateral target conditions elicit an N2pc component. Moreover, N2pc amplitude is reduced in the together conditioned compared to the alone condition. Accordingly, there was both a main effect of object type, $F(1,15) = 9.77$, $p < 0.01$, $\eta_p^2 = 0.39$, and a main effect of competition, $F(1,15) = 5.85$, $p < 0.05$, $\eta_p^2 = 0.28$. In contrast, the interaction ($F < 1$) was not statistically significant. The one-sample *t*-tests confirmed that a significant N2pc was only elicited by the targets: lateral target alone, $t(15) = -3.01$, $p < 0.01$; lateral target with decoy, $t(15) = -2.28$, $p < 0.05$; lateral decoy alone, $t(15) = -1.38$, $p = 0.19$; lateral decoy with target, $t(15) = 1.73$, $p = 0.10$.

A Ptc component was elicited in all conditions, but Ptc amplitude is greater in amplitude when only one color singleton was present in the display compared to when the target and decoy were presented together (Figures 8 and 9). Accordingly, there was a main effect of competition, $F(1,15) = 5.86$, $p < 0.05$, $\eta_p^2 = 0.28$. Neither the main effect of object type nor the interaction was not statistically significant (*F*s < 1). The one-sample *t*-tests revealed that a significant Ptc component was elicited when the lateral decoy was alone, $t(15) = 5.29$, $p < 0.01$, or presented together with the target, $t(15) = 4.10$, $p < 0.01$. In addition, when the lateral target was presented alone a significant Ptc

component was elicited, $t(15) = 3.30$, $p < 0.01$. When the lateral target was presented with the decoy, the Ptc component was only marginally reliable, $t(15) = 1.90$, $p = 0.077$.

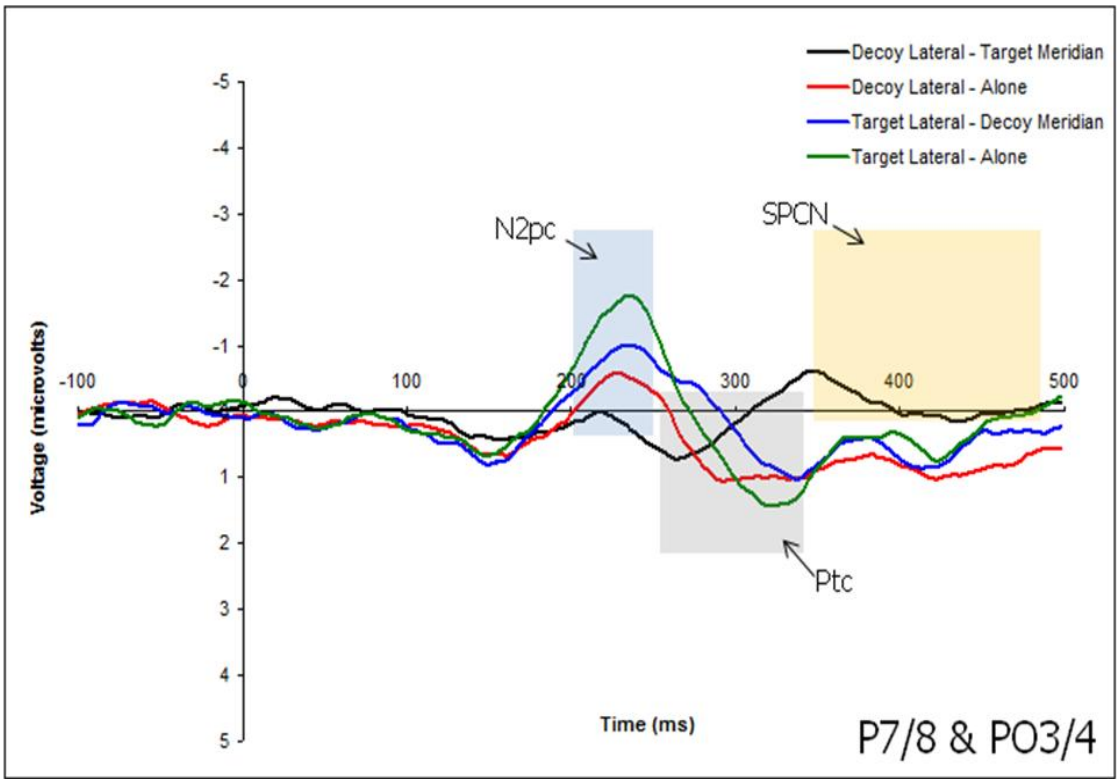

Figure 8. Contralateral minus ipsilateral difference waveforms for Experiment 2. These difference waveforms were calculated by subtracting the waveforms ipsilateral to the target and decoy from the waveforms contralateral to the target and decoy. Only the targets elicited an N2pc component and the amplitude of the N2pc component is reduced for the together compared to the alone condition. A Ptc component is evident in all conditions. Finally, there was no SPCN elicited in any condition.

As can be seen in Figures 8 and 9, there was not an SPCN component elicited in any condition. In contrast, there is a sustained contralateral *positivity* during the SPCN time window that varies by condition. In confirmation of this observation, there was a main effect of competition, $F(1,15) = 10.73$, $p < 0.01$, $\eta_p^2 = 0.42$, which was qualified by a statistically significant interaction between object type and competition, $F(1,15) = 16.43$, $p < 0.01$, $\eta_p^2 = 0.52$. In contrast, the main effect of object type was not statistically

significant (F <1). The one-sample t-tests revealed a significant contralateral positivity for the lateral target with decoy, $t(15) = 2.39$, $p < 0.05$, and for the lateral decoy alone, $t(15) = 4.40$, $p < 0.01$. The lateral target alone elicited a marginally reliable contralateral positivity, $t(15) = 2.06$, $p = 0.058$. The lateral decoy with target did not elicit any reliable activity, $t(15) = -0.85$, $p = 0.411$.

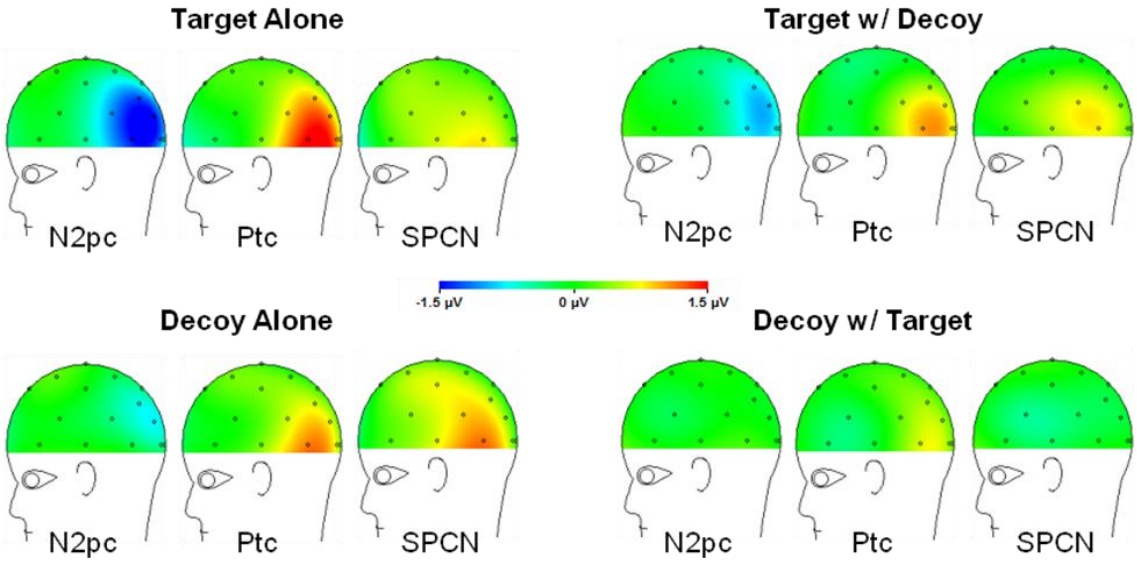

Figure 9. Scalp topographies for Experiment 2. The N2pc component has a typical posterior topography over the contralateral scalp. The Ptc component is also distributed over the posterior scalp but is slightly more anterior than the N2pc. Activity in the SPCN interval manifests as a contralateral positivity that is more anterior than the N2pc and is similar to the Ptc component in distribution.

Discussion

Experiment 2 sought to investigate the degree to which top-down biasing can influence competition and selectivity in visual search. Participants responded to the orientation of a target color singleton (a green or orange letter T) when it was present in the display, and ignored a decoy color singleton (letter L in the opposite color of the target) when it was present in the display. Critically, participants knew the color of the

target in advance. The target or the decoy was presented in the left or right visual field while the other object, if present, was placed on the vertical meridian so that only the lateral stimulus would contribute to the lateralized ERP components (i.e., the N2pc, Ptc, and SPCN components). Competition between the objects was manipulated by presenting the target or decoy alone or presenting the target and decoy together.

The N2pc results are markedly different than those obtained in Experiment 1. First, only the lateral target conditions elicited a significant N2pc component. The lack of N2pc for the lateral decoy conditions suggests that the decoy does not capture attention when participants know the color of the target and decoy in advance. However, the N2pc component elicited by the lateral target is reduced in amplitude when the decoy is present compared to when the target is alone. Thus, even if the decoy does not capture attention, the decoy does still influence target processing through suppressive interactions. Overall, this suggests that knowledge of the target color reduces attentional capture by the decoy, but this top-down bias cannot completely eliminate processing of the decoy or its suppressive influence on the target.

The Ptc results are unlike previous studies and raise questions about the functional significance of the Ptc component. First, both the target and decoy elicited a Ptc component. In contrast, in both Experiment 1 and a previous experiment (Hilimire et al., 2011), only the decoy elicited a significant Ptc component. Because the Ptc component seemed to be elicited only by distractors, I had previously interpreted the Ptc component as indexing suppression of the distractor (Hilimire et al., 2011). If the Ptc component indexes suppression, it is unclear why it is elicited by the target in Experiment 2. However, it is possible that because participants knew the target color in advance and had

much faster reaction times as a result, they had already completed processing the target and disengaged processing of the target. Under this interpretation, the Ptc component might index something like inhibition of return or disengagement of attentional processes once an object is either fully processed or identified as task-irrelevant. Future studies could try to directly link the behavioral magnitude of inhibition of return to Ptc amplitude to examine this possibility.

Second, Ptc amplitude was greater when the target or decoy was presented alone compared to when both salient objects were presented together. In other words, Ptc amplitude *decreased* with increased competition. In contrast, in Experiment 1 and in previous experiments (Hilimire et al., 2009; 2010), Ptc amplitude *increased* with competition. Thus, the Ptc component is much more complex than previously interpreted, and may in fact index multiple processes, or something completely different than suppression or disengagement. Future studies should examine how the Ptc component varies with different manipulations of competition (e.g., target-decoy similarity) and different types of top-down biasing (e.g., knowledge of target location) to further elucidate the functional significance of the Ptc component.

The SPCN results in Experiment 2 also draw into question the functional significance of the activity in the SPCN time window. Instead of a sustained posterior contralateral negativity (SPCN), a contralateral *positivity* was observed in Experiment 2. Typically, the SPCN is interpreted as reflecting visual short-term memory activation (e.g., Emrich, Al-Aidroos, Pratt, & Ferber, 2009; Robitaille & Jolicoeur, 2006). If a contalateral negativity is indicative of memory, it is unclear how a contralteral positivity should be interpreted. However, one possibility is that the inhibition of return or

disengagement as possibly indexed by the Ptc component may simply be persisting through the SPCN interval. Again, future studies could try to directly link the behavioral magnitude of inhibition of return to activity in the SPCN interval to examine this possibility.

The results of Experiment 2 corroborate previous findings from a similar paradigm. Kiss, Grubert, Petersen, and Eimer (2011) measured the ERPs elicited by targets and distractors in an additional singleton paradigm. In their version of this paradigm, the objects were either all circles or all diamonds except the target which was the opposite shape. Thus, the target was defined as the shape singleton. In addition, the objects were either all red or all green except the distractor. Thus, the distractor was defined as the color singleton. Observers indicated whether a line inside the shape singleton was vertical or horizontal. They manipulated competition by presenting only the color singleton (i.e., the distractor) or only the shape singleton (i.e., the target) on some trials compared to presenting both singletons together on other trials.

Kiss and colleagues (2011) found that a lateral distractor when presented without the target did not elicit an N2pc component. On the other hand, they found that the lateral distractor elicited a contralateral *positivity* in the N2pc interval when the target was present on the vertical meridian. This corresponds to the results of Experiment 2 in that the decoy did not elicit an N2pc component in either condition. Rather, both lateral decoy conditions elicited a Ptc component which seemed to onset sooner when the target was also present in the display (see Figure 7). Kiss and colleagues (2011) concluded from their results that the color singleton does not capture attention. However, they also noted that reaction times were slowed when the color singleton was present in the

display. This suggested to them that the decoy was still influencing the target through mutually suppressive competitive interactions. However, they did not include the condition necessary to show this physiologically. In particular, their design did not include trial types where the target was lateralized and the distractor was on the midline. Experiment 2, however, did include this condition and demonstrated that the N2pc component elicited by the lateral target was reduced in the presence of the midline decoy. Thus, the results of Experiment 2 confirm that the color singleton distractor, while not capturing attention, still influenced the target via suppressive interactions.

CHAPTER 4

EXPERIMENT 3

In Experiments 1 and 2, the ERP components were elicited by lateralized color singletons. Therefore, it is possible that the lateralized ERP components may actually reflect low-level sensory differences rather than attentional factors due to the fact that there was a color singleton in one visual field but only gray objects in the other visual field. To control for this possibility, all of the objects in Experiments 1 and 2 were equated on luminance, which has been shown to be effective in eliminating sensory confounds in the past (Hickey et al., 2009; Hilimire et al., 2009; Sawaki & Luck, 2010). However, Experiment 3 was designed to more definitively eliminate this alternative explanation.

In Experiment 3, the stimulus displays were identical to those of Experiment 1. However, in Experiment 3, participants performed a search task on the four small squares presented at fixation. Specifically, participants reported the orientation of the gap in the target square. The addition of this task has been shown to eliminate lateralized ERP components in a previous study (Sawaki & Luck, 2010). If the lateralized ERP responses in Experiments 1 and 2 were due to attentional processing of the lateral target or decoy, no lateralized ERP components should be observed when participants are attending the task at fixation. On the other hand, if the lateralized ERP components were due to low-level sensory imbalances between the left and right visual fields, then identical lateralized ERP components should be observed in Experiments 1 and 3.

Method

The method was similar to Experiment 1 with the following changes.

Participants

16 undergraduate students (aged 18-44 years, M = 21.2 years, SD = 6.2 years) participated for course credit.

Stimuli and Design

The stimulus displays were identical to Experiment 1.

Procedure

The procedure was identical to Experiment 1 with the following change. The participants were instructed to report whether the gap in the target square presented at fixation appeared at the top or the bottom as quickly as possible while maintaining approximately 90% accuracy. Responses were given using the number pad of a standard keyboard using the right hand (‘1’ for top with right index finger, ‘2’ for down with right middle finger).

Electrophysiological Recording and Analysis

Recording and analysis was identical to Experiment 1. Participants were replaced if their average remaining HEOG activity exceeded ±3.2 μV (2 participants were replaced). The grand average HEOG of the participants included in the analysis did not exceed ±2.0 μV.

Results and Discussion

The difference in reaction time between the conditions where the target and decoy were presented together (M = 520.06 ms, SD = 73.13 ms) compared to when the target was presented alone (M = 516.23 ms, SD = 72.83 ms) was only marginally reliable, $t(15) = 1.95$, $p = 0.070$. Proportion correct was not significantly different when the target and decoy were presented together (M = 0.93, SD = 0.04) compared to when the target was presented alone (M = 0.93, SD = 0.04), $t(15) = 0.63$, $p = 0.54$.

As can be seen in Figure 10 lateralized activity did not vary by condition for the N2pc component (Fs < 1.67, ps > 0.22), Ptc component (Fs < 2.72, ps > 0.12), or the SPCN component (Fs < 2.85, ps > 0.11). Thus, it is safe to conclude that the results from Experiments 1 and 2 are due to attentional processes rather than low-level sensory differences.

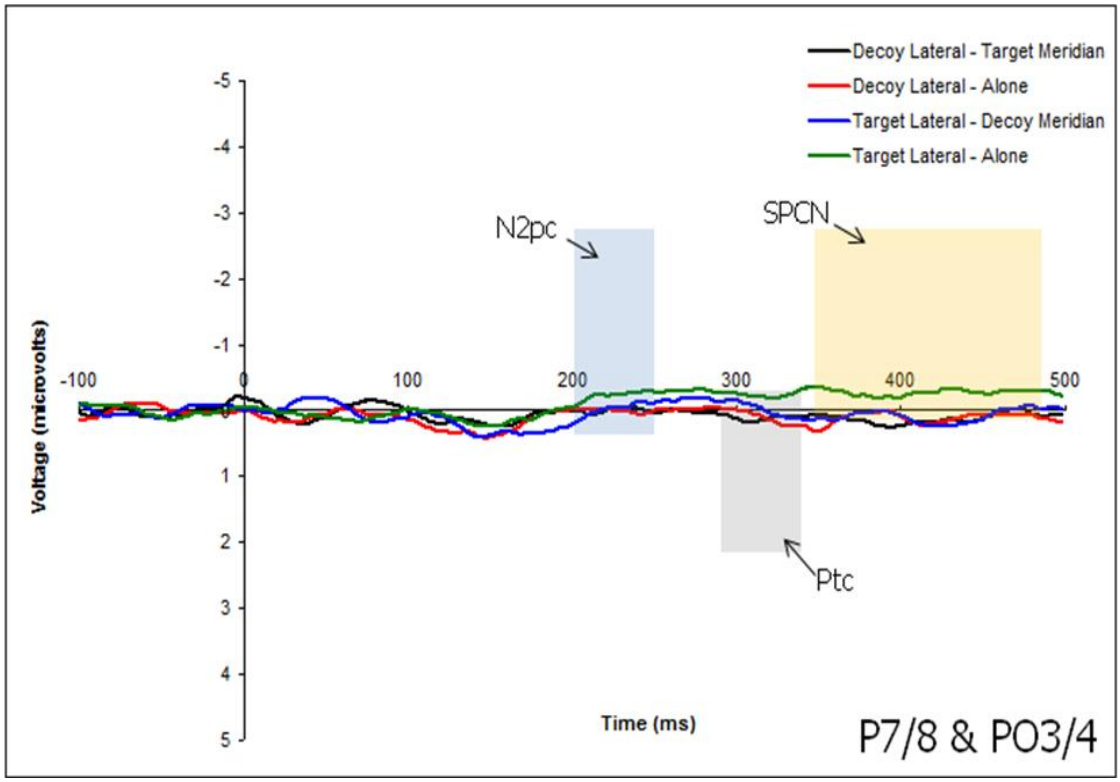

Figure 10. Contralateral minus ipsilateral difference waveforms for Experiment 2. These difference waveforms were calculated by subtracting the waveforms ipsilateral to the target and decoy from the waveforms contralateral to the target and decoy. There was no variation of lateralized activity by condition in Experiment 3.

CHAPTER 5

GENERAL DISCCUSION

In three experiments, I investigated the degree to which competition and selectivity in the visual system influences the processing of task-relevant and task-irrelevant objects. In the first two experiments, observers completed a target-decoy task. In this task, one or two color singletons were presented amongst gray filler objects. Observers discriminated the orientation of the color singleton target and ignored the color singleton distractor. Competition was manipulated by varying whether one or two color singletons were present in the display with the assumption that more competition would occur when two singletons were present.

In these experiments, I used lateralized event-related potentials (ERPs) as the dependent measures, including the N2pc, Ptc, and SPCN components. By arranging the stimulus displays such that one color singleton was presented at a lateral location while the other color singleton (if present) was presented on the vertical meridian, it was possible to associate any lateralized ERP activity with the lateralized stimulus (Hickey et al., 2009; Hilimire et al., 2011; Woodman & Luck, 2003b). This way, I was able to obtain separate measures for the task-relevant singleton (the target) and the task-irrelevant singleton (the decoy). Overall, the goal was to examine the temporal dynamics of target and distractor processing, and how these dynamics were affected by competition between the objects and by top-down biasing.

In Experiment 1, participants did not know the color of the target before the trial began. The target was instead based solely on its form; the target was the letter T and the

decoy was the letter L. In Experiment 2, I introduced an additional top-down factor to bias the competition toward the target. Specifically, I informed observers of the target color in advance. Experiment 3 addressed a potential low-level sensory explanation for the results obtained in Experiments 1 and 2. In this experiment, observers performed a difficult visual search task at fixation to confirm that the lateralized ERPs are only elicited when participants attend to the peripherally presented target or decoy color singleton.

The behavioral and N2pc results of these experiments inform a debate in the literature regarding whether top-down information can influence attentional capture by task-irrelevant but bottom-up salient objects. At one extreme, Theeuwes (2010) states that attentional capture is completely determined by bottom-up factors. According to Theeuwes, top-down information can only speed the disengagement of attention once attention is initially captured by bottom-up salient objects. At the other extreme, Folk, Remington, & Johnston (1992) state that attentional capture is contingent on top-down information. That is, even if an object is bottom-up salient, it will only capture attention if it is congruent with current goals.

Here, the behavioral results showed that participants performed worse when the color singleton decoy was present concurrently with the target compared to when the color singleton target was presented alone. This phenomenon is called the additional singleton effect when obtained in similar visual search paradigms (e.g., Theeuwes, 1991). Traditionally, the additional singleton effect is interpreted as an indication that the color singleton distractor has captured attention. Attention must then be disengaged from the distractor so that the target can be selected. Because this capture, disengagement, and

shift of attention to the target take time, observers are slower to respond. I showed that the additional singleton effect can be influenced by top-down information. In Experiment 1, when participants *did not* know the color of the target, the additional singleton increased reaction times by about 73 ms. In Experiment 2, when participants *did* know the color of the target, the additional singleton only increased reaction times by about 13 ms. Thus, it seems that the top-down information about the target color influenced the amount of interference from the singleton distractor.

The N2pc results also help address the debate regarding top-down contingent attentional capture. In Experiment 1, both the target and the distractor elicited an N2pc component when the target color was unknown. In contrast, the distractor did not elicit an N2pc component when the target color was known in Experiment 2. The results also showed that N2pc amplitude is reduced when both salient objects are presented together. Critically, this occurred even when the target color was known in Experiment 2. That is, even though the distractor did not elicit an N2pc in Experiment 2, the presence of the distractor still reduced the N2pc elicited by the target (see also Kiss et al., 2011). If the N2pc component indexes the initial attention processing (i.e., attentional capture by salient objects), then the results suggest that top-down information can prevent attentional capture by irrelevant but bottom-up salient objects. However, the results also show that the distractor can still influence the target because the target elicited N2pc was reduced in amplitude when the decoy was concurrently presented. This suggests that the small behavioral additional singleton effect in Experiment 2 might be due to mutually suppressive competitive interactions between the color singletons rather than attentional capture by the irrelevant singleton (cf., Kiss et al., 2011). With this interpretation, the

results support the contingent capture theory. That is, only the singleton that matched top-down knowledge captured attention. However, the results also show that task-irrelevant salient singletons can still interfere even if they don't necessarily capture attention.

There is an alternative interpretation of the reduction of the additional singleton effect shown in Experiment 2. Pinto, Olivers, & Theeuwes (2005) have demonstrated that intertrial priming of the target color or distractor color can account for variability in the additional singleton effect. When the color of the target on the current trial matches the color of the target on the previous trial, participants are faster to respond. When the color of the target on the current trial matches the color of the distractor on the previous trial, participants are slower to respond. In other words, participants enhance processing of the previous target color and inhibit processing of the previous distractor color due to intertrial priming. Pinto and colleagues (2005) argue that this intertrial priming can completely account for the additional singleton effect.

This intertrial priming account could explain why the singleton distractor did not capture attention in Experiment 2. In Experiment 1, participants did not know the color of the target or decoy in advance. Practically, this means that the color of the target changed randomly between orange and green on each trial. Thus, on about half the trials the color of the target on the current trial matched the color of the distractor on the previous trial. In this case, the target color would be inhibited and the distractor color would be primed, resulting in attentional capture by the distractor singleton. These types of trials are likely driving the large additional singleton effect in Experiment 1. On the other hand, when participants knew the color of the target in advance in Experiment 2,

the color of the target was the same on each trial. This means that on every trial the color of the target was primed and the color of the distractor was inhibited. This could explain why the distractor singleton did not capture attention in Experiment 2. With this interpretation, the contingent capture account is not supported because the concept of top-down knowledge is not necessary to explain why the additional distractor singleton did not capture attention in Experiment 2. In the future, experiments should cue the target color on a trial by trial basis and explicitly examine attentional capture on trials where the target color switches compared to when the target color stays the same. Only through trial by trial cuing can this alternative intertrial priming account be tested.

The Ptc component results serve to raise more questions than they answer. In Experiment 1, when the target color was unknown, only the distractor elicited a Ptc component. On the other hand, both the target and the distractor elicited Ptc components when the target color was known in Experiment 2. Previously, when the Ptc had only observed in response to distractors (Hilimire et al., 2011), I had interpreted the Ptc component as reflecting suppression of the distractor. Yet, in Experiment 2, targets elicited a Ptc component. Why would observers suppress the target? One possibility is that the Ptc component indexes something like inhibition of return (Posner & Cohen, 1984). Once an object is processed, its location is inhibited so that attention does not return to that object immediately. In Experiment 2, when observers had relatively quick reaction times (approximately 432 ms), it is possible that they had already finished discriminating the target by the time the Ptc component occurs (approximately 325 ms). Once the orientation of the target is discriminated, the location of the target is inhibited as indexed by the Ptc. However, if the Ptc does index inhibition of return, it remains

unknown why Ptc latency proceeds the manual button press response by roughly 100 ms. One possibility is that those 100 ms are used for response selection and execution while attention can shift elsewhere. To further test this interpretation of the Ptc component, future studies can manipulate inhibition of return and determine if the behavioral magnitude of inhibition of return relates to Ptc component amplitude.

The SPCN results also raise questions about the functional significance of the activity in this interval. Typically, the SPCN is interpreted as reflecting visual short-term memory activation (e.g., Emrich, Al-Aidroos, Pratt, & Ferber, 2009; Robitaille & Jolicoeur, 2006). Here, an SPCN component was only elicited by the target when the color of the target was unknown (Experiment 1) and when the distractor was present in the display. On the other hand, a contralateral *positivity* was elicited in Experiment 2 during this interval. One possibility is that activity in this late interval can index either continued processing of the target (i.e., representing the target in visual short-term memory), or it can index continued inhibition of the previously processed location. In the case of Experiment 1, continued processing of the target occurred during this interval because observers did not know the color of the target in advance and they had to overcome competition from the salient distractor. This continued processing was reflected in a contralateral *negativity* that is typically called the SPCN component. In the case of Experiment 2, observers had already processed the target and inhibited its location, assuming the interpretation of the Ptc component above is correct. The contralateral *positivity* observed in Experiment 2 during this interval might simply reflect the continued inhibition of that location.

Taken together, the results can be informally modeled with an implementation of the biased competition principles that combines elements of the Selective Tuning Model (Tsotsos, 1990) and elements of feedforward models (e.g., FeatureGate; Cave, 1999). First, there is a hierarchical structure that mimics the visual system. At the input level, there are cells with small receptive fields that feed into higher-level cells with larger receptive fields. At each level, there is localized competition for representation between the objects to determine which object features are passed to the next level. This competition occurs via mutually suppressive competitive interactions between object representations. Objects that are bottom-up salient or match top-down information will progress through the hierarchy to the top levels. If more than one object makes it to the top layer, those objects attempt to prune each other's inputs until only one object is represented. Once an object loses the competition, its location is inhibited. This results in boosting of the target signal because the other object no longer exerts a suppressive influence on the target representation. Once the winning object is finished processing, its location is inhibited as an inhibition of return mechanism.

In this model, the N2pc component may map onto activity of intermediate layers in the hierarchy based on its localization in occipitotemporal cortex. Depending on the timing of the feedforwad and feedback traversals, the N2pc could reflect two possible aspects of the model. Because the N2pc is reduced by competition between salient objects (Experiments 1 & 2; Hilimire et al., 2009; 2010), the N2pc might be reduced by competition between the objects during the feedforward pass. This interpretation means that the N2pc reflects representation of objects and that these representations are affected by competitive interactions within a level of the hierarchy to determine which object is

passed on to the next level. On the other hand, reduced N2pc amplitude might reflect competition in the feedback traversal. In this interpretation, when two color singletons make it to the top layer, they both attempt to inhibit each other's input to the top-layer. Reduced N2pc amplitude might reflect these feedback inhibitory influences on the object representations. Once the timing of feedforward and feedback traversals are better specified, it may be possible to determine which alternative is more likely by comparing the onset of the N2pc component to those estimates of feedforward and feedback timing.

The Ptc component might map onto the inhibition of return mechanism of the model. According to this account, the two salient singletons will make it to the top of the hierarchy and then attempt to inhibit each other's input. Once the irrelevant object loses the competition, its location is inhibited which is indexed by the Ptc component. Once the target is processed, its location is also inhibited which is also indexed by the Ptc component. It is also certainly possible the activity in the Ptc interval does not reflect a unitary psychological process; the Ptc elicited by irrelevant objects indexes processes completely different from those reflected in the Ptc elicited by relevant objects.

Finally, the SPCN might reflect enhanced target processing. Once the irrelevant objects are inhibited, and if the task is not yet complete, processing of the task-relevant object can continue without the suppressive influence of the irrelevant singleton. On the other hand, the contralateral positivity in this interval may reflect continued inhibition of a previously processed object.

In summary, I examined three lateralized components of the event-related potential – the N2pc, Ptc, and SPCN – as indices competition and selectivity in the visual system. Participants responded to the orientation of a color singleton target while

ignoring a color singleton distractor. Competition between the objects was manipulated by presenting visual search arrays that contained only a target, only a distractor, or both objects together. In Experiment 1, observers did not know the color of the target in advance, whereas in Experiment 2, this information was provided. Experiment 3 was a control experiment to rule out low-level sensory explanation of the effects obtained in the previous experiments. The results showed that both target and distractor elicited an N2pc component when target color was unknown, but the distractor did not elicit an N2pc component when the target color was known. Moreover, N2pc amplitude is reduced when both salient objects are presented together. I have argued that when participants have top-down knowledge, they can prevent attentional capture by irrelevant salient singletons. However, intertrial priming is also a viable alternative explanation of the results, and this must be tested in a future experiment where target color is cued on a trial by trial basis. The Ptc and SPCN results challenge previous interpretations of the functional significance of these components. When the target color is unknown, only the distractor elicits a Ptc component, but both target and distractor elicit a Ptc when the target color is known. This challenges the previous interpretation of the Ptc component as an index of distractor suppression. I have suggested that the Ptc component may still index an inhibitory mechanism akin to inhibition of return, but future studies will need to explicitly test this idea. An SPCN component was only elicited by the target when the color of the target was unknown and the distractor was present in the display. On the other hand, when the target color was known a contralateral positivity emerged in this interval. Typically, the SPCN is interpreted as reflecting representation of objects in

visual short-term memory. Future studies should examine the significance of the contralateral positivity in this interval.

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